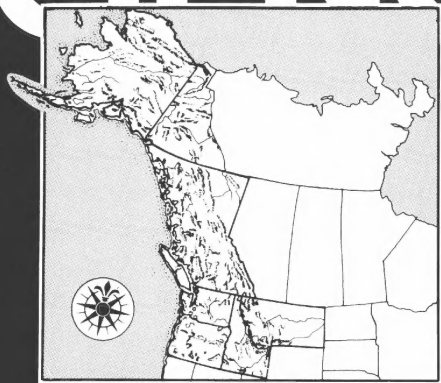


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SEED BANKS IN OLD-
GROWTH FOREST

NORTHWEST SCIENCE



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Annual Meeting of the Northwest Scientific Association

The 67th Annual Meeting of the Northwest Scientific Association will be held on March 24-26, 1994, at Central Washington University in Ellensburg, Washington. Additional participating organizations include the Northwestern Association of Vertebrate Biology, Association of Washington Geographers, Rare Plant Consortium, and Northwest Lichen Guild.

Symposia are currently planned on: the shrub-steppe ecosystem, natural resources of the Yakima River Basin, and research in forest canopies. Several field trips will focus on the geology, vegetation, and wildlife of central Washington. The meeting will also feature a lichen identification workshop and a demonstration of applications in photogrammetry. Pat O'Hara, renowned wildlife and nature photographer, will be the guest speaker at the banquet, and give a presentation on the Beringian Heritage International Park.

All those interested in science and resource management issues in the Pacific Northwest are invited to attend. Students are especially encouraged to attend and present papers in a variety of subject areas. For information and registration materials, please contact Dr. Bill Barker, Biology Department, Central Washington University, Ellensburg, WA 98926 (USA); telephone 509-963-2731; fax 509-963-1047.

New Associate Editors for *Northwest Science*

Each paper submitted to *Northwest Science* is assigned to one of the Associate Editors listed on the contents page of the journal. The Associate Editors are responsible for obtaining technical reviews, compiling review comments, and evaluating the merit of each manuscript. Both technical expertise and organizational skill are required to provide effective and timely reviews.

Northwest Science welcomes three new Associate Editors to the journal's editorial board: Eldon H. Franz, Washington State University (Botany); R. Gerald Wright, University of Idaho (Wildlife Biology); Richard Forbes, Portland State University (Zoology).

The former Associate Editors in these subject areas are: Mark V. Wilson, Oregon State University (Botany); Margaret O'Connell, Eastern Washington University (Wildlife Biology); Barry L. Keller, Idaho State University (Zoology). Each of these scientists spent several years as Associate Editor. The Editor would like to thank them for their dedicated service to *Northwest Science*, and for their professionalism in evaluating manuscripts for the journal.

Heat-Treatment Effects on Seed Bank Species of an Old-growth Douglas-fir Forest

Abstract

Although many studies have investigated the density and species composition of soil seed banks, few studies have investigated the effect of disturbance on seed banks. An earlier field study (Clark 1991) showed that the density of buried seeds of an old-growth Douglas-fir forest after logging and slash-burning was significantly less than the seed bank density of an adjacent, undisturbed old-growth Douglas-fir forest. The purpose of the present study was to investigate the mechanisms for this seed bank reduction. Six species found in the old-growth seed bank received experimental heat treatments that included six combinations of temperature, duration and soil moisture. Generally, germination percentages were not significantly affected when seeds were heated at 50C for one hour in either the wet or dry soil, but were significantly reduced at 100C for 15 min in both the wet and dry soils. When the seeds were heated at 75C for 15 min, germination was significantly reduced in the wet soil only. Because of the seeds' sensitivity to heat, few of these seed bank species are likely to be available for establishment after fire, even one of low intensity. This experimental study supports the hypothesis that seed mortality from elevated temperature during fire reduced seed bank densities of the old-growth forest and does not support the hypothesis that the reduction was due to stimulation of germination by heat. Although this study tested species with different growth forms and longevities, germination responses were generally the same for all species.

Introduction

Substantial numbers of dormant seeds have been found in the soil of most habitats (Leck *et al.* 1989). This soil seed bank provides an immediate source of propagules for revegetation after disturbance (Roberts 1981, Pickett *et al.* 1987). The persistent seed bank also maintains a reservoir of genotypes that can provide substantial flexibility to environmental changes, buffering the population from extinction and preserving the species within a community (Templeton and Levin 1979). Although numerous studies have investigated the seed density and species composition of soil seed banks (Leck *et al.* 1989), relatively few studies have investigated the effect of disturbance on seed bank density and composition (Roberts and Dawkins 1967, Uhl *et al.* 1981, Mallik and Gimmingham 1985, Smith and Kadlec 1985, Hassan and West 1986, Kauffman 1986). High temperatures from fire generally lower the seed bank density either by seed mortality or by heat-stimulated seed germination, thus favoring the survival of species with heat-resistant seeds or with seeds that are stimulated to germinate by heat.

Both natural fires and slash-burning after clear-cut harvesting are important disturbances in the coniferous forests of the Pacific Northwest. We recently compared the seed bank density and composition of a recently disturbed old-growth Douglas-fir forest with the seed bank of an adjacent undisturbed old-growth Douglas-fir forest

(Clark 1991). The disturbed site was logged in late fall 1985 and the slash burned with a low-intensity fire in July, 1986. Temperatures of the mineral soil during the fire were between <52C and 177C at the surfaces, between <39C and 139C at 2 cm, between 52C and 66C at 4 cm, and <52C at 6 cm (M. V. Wilson, unpublished data). (The duration of the temperature exposure was not measured.) Seed bank samples collected the following spring showed that the disturbed seed bank density (18.4/m²) was significantly less than the old-growth seed bank (88.6 seeds/m²) (Clark 1991).

The purpose of the present study was to investigate the mechanisms for this seed bank reduction using an experimental approach in a controlled laboratory setting. The specific objective was to determine the response of seeds to various temperatures, durations of heating, and soil conditions (wet or dry).

Study Species

All herb and shrub species found in the soil seed bank of an old-growth Douglas-fir forest (Clark 1991) were selected for experimental heat treatment except for Watson's willow-herb (*Epilobium watsonii*), soft rush (*Juncus effusus*), and Pacific blackberry (*Rubus ursinus*), which were not included because of difficulty in germinating the seeds of these species. The remaining six study species included an early successional annual, wood groundsel (*Senecio sylvaticus*), an early

successional biennial, common thistle (*Cirsium vulgare*), two herbaceous perennials, Dewey's sedge (*Carex deweyana*) and fireweed (*Epilobium angustifolium*), and two old-growth woody understory species, western rhododendron (*Rhododendron macrophyllum*) and salal (*Gaultheria shallon*). Four of these species, *Gaultheria shallon*, *Rhododendron macrophyllum*, *Epilobium angustifolium* and *Senecio sylvaticus*, are also important components of the initial vegetation following disturbance by logging (Dyrness 1973, Halpern 1989, Clark 1991). Little information is known about seed densities at different soil depths and the seed longevity of these species in old-growth Douglas-fir forest seed banks (Kellman 1970, 1974).

Evidence from an earlier study (Clark 1991) showed that relatively few individuals established from seed the first year after disturbance at the study site. Kellman (1974) suggests that only logged sites contiguous to an established early successional community would receive appreciable migrant seed of early successional species due to the inefficient movement of these species' seeds through forest stands. Since our site was not adjacent to such seed sources, a large portion of the few individuals establishing from seed the first year probably came from seed bank propagules. The second year after disturbance brought a tremendous increase in individuals establishing from seed (Clark 1991). The source of these seeds was probably on-site seed dispersal from the few annuals establishing from seed in the first year, particularly *Senecio sylvaticus*. Thus, although seed bank densities were low compared to other forests (Strickler and Edgerton 1976, Moore and Wein 1977, Kramer and Johnson 1987, Morgan and Neuenchwander 1988, and Fyles 1989), plants establishing from the seed bank might strongly influence revegetation starting in the second year after disturbance.

Methods

Seeds were collected at maturity from plant populations growing at the study site located in the H.J. Andrews Experimental Forest, a National Science Foundation Long-Term Ecological Research Site in the western Cascade Mountains of Oregon. The collection site, about 800 m elevation, was dominated by old-growth western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*) with some western redcedar (*Thuja plicata*).

The understory included dwarf Oregon grape (*Berberis nervosa*), twinflower (*Linnaea borealis*), red huckleberry (*Vaccinium parvifolium*), *Rhododendron macrophyllum* and *Gaultheria shallon*. The habitat-type is classified as western hemlock/rhododendron/dwarf Oregon grape (Dyrness *et al.* 1974). After seed collection in the summer of 1988, the seeds were stored dry at 4C until experimental treatments were conducted in early 1990. Preliminary germination tests necessitated this schedule.

Experimental treatments included six combinations of temperature, duration and soil moisture: seeds heated in dry soil at 50C for one hour, 75C for 15 min and 100C for 15 min, and seeds heated in moist soil at the same three temperatures and durations. These conditions were selected to match soil temperature data collected during the 1986 slash burn following logging near the site (M. V. Wilson, unpublished data) and to match moisture extremes found between the wetter soils of spring and late fall and the drier soils of summer.

For each heat treatment, two test tubes (2.5 cm diameter x 15 cm deep) per species were placed in a water bath. Each tube was filled with 20 seeds mixed with approximately 15 cm³ dry soil; 10 ml of water was added to the second tube 3 minutes before being placed in the water bath. (For *Cirsium vulgare*, 10 seeds were used in each test tube). This procedure was replicated five times per experimental treatment. These methods are modifications of methods commonly used by other researchers investigating heat effects on seed germination (Gratkowski 1962, Keeley *et al.* 1985, Mallik and Gimingham 1985, Kauffman 1986, Bell *et al.* 1987, Keeley 1987).

In preliminary tests, thermistors were placed at four locations in a test tube filled with 15 cm³ soil: at the surface, in the center midway down the tube, along the side next to the glass midway down, and at the bottom. Temperatures were recorded during each of the six experimental conditions. These tests showed that (a) it took approximately 7-10 min for the soil temperature in the test tubes to equilibrate, (b) the temperature of the soil at equilibrium was the same as the temperature of the water bath, with the exception of the dry soil, which was 98C at the 100C treatment, and (c) the soil temperature after equilibration was uniform throughout the test tube during each treatment.

After each heat treatment the contents of each test tube were emptied into a Petri dish. In addition, to make sure no seeds were left behind, the residues in the test tubes with wet soil were rinsed with distilled water, filtered, air dried and added to the appropriate Petri dish. Five controls (no heat treatment) for each species were treated identically as the experimental treatments; that is, the same procedures for transferring soil and seeds were followed for the controls as were used for the experimental treatments.

The Petri dishes were placed in a controlled environment with 14 hours of light and moistened with distilled water as needed. Preliminary tests showed that *Gaultheria shallon*, *Senecio sylvaticus* and *Rhododendron macrophyllum* germinated best with alternating temperatures of 20C for 14 hours and 15C for 10 hours. The other species germinated best at alternating temperatures of 30C for 14 hours and 20C for 10 hours. Therefore, these temperatures were used to promote germination. The number of germinating seeds was counted until no new germination occurred for at least 14 days. Seeds were considered germinated when the shoot could be seen.

Differences in final germination rates between treatments and controls were tested for statistical significance with a Mann-Whitney test (Conover 1980).

Results and Discussion

For five of the six species, germination percentages were not significantly affected compared to un-

heated controls when seeds were heated at 50C for one hour in either the wet or dry soil (Table 1). The single exception was *Epilobium angustifolium* for which germination was significantly reduced in the wet soil at 50C. Germination percentages of all six species were significantly reduced at 100C for 15 min in both the wet and dry soils (Table 1). When the seeds were heated at 75C for 15 min, germination was significantly reduced in the wet soil only. No treatment produced significantly higher germination than the control. Thus, seeds of these seed bank species appear to be killed at the relatively low temperatures of 75C and 100C, with the effect stronger in wet soil.

Several factors may explain why the wet and dry soil treatments differed at 75C. The increased seed mortality with wet soils might have been due to increased heat conductivity through the moist seed coats, causing death of interior seed tissue. The seeds in the wet soil could also have imbibed more water than those in the dry soil. Seeds, particularly those of herbaceous species, that absorb moisture beyond 20% of their dry weight can be quite sensitive to heat (Parker and Kelly 1989), possibly because enzymes are more susceptible to heat denaturation when hydrated than when dry (Salisbury and Ross 1985). Although preliminary tests at 75C showed that dry and wet soils differed little in temperature, the wet soil at 75C took an average of about 9 min to cool to 50C after removal from the water bath compared to the average time of 5 min for the dry soil; thus, more seeds could

TABLE 1. Mean seed germination percentages following experimental heat treatments of six species found in the seed bank of an old-growth Douglas-fir forest. The treatments were: W50, 50C for 60 min in wet soil; W75, 75C for 15 min in wet soil; W100, 100C for 15 min in wet soil; D50, 50C for 60 min in dry soil; D75, 75C for 15 min in dry soil; D100, 100C for 15 min in dry soil; and CON, control. n=5. Differences in germination percentages between treatment and control were tested using the Mann-Whitney test.

SPECIES	TREATMENTS						
	W50	W75	W100	D50	D75	D100	CON
<i>Carex deweyana</i>	85	0**	0**	89	89	0**	89
<i>Cirsium vulgare</i>	34	0**	0**	44	32	6*	62
<i>Epilobium angustifolium</i>	0**	0**	0**	26	30	0**	20
<i>Gaultheria shallon</i>	21	0**	0**	20	10	1**	17
<i>Rhododendron macrophyllum</i>	37	0**	0**	33	48	2**	41
<i>Senecio sylvaticus</i>	72	0**	0**	72	76	29**	87

* $P < 0.05$

** $P < 0.01$

have been killed because of the longer temperature durations.

Germination percentages of all species were significantly reduced after heating to 100C in both wet and dry soils. This experimental study thus supports the hypothesis that the general reduction in the mean seed bank density after logging and slash-burning of the old-growth Douglas-fir forest (Clark 1991) was caused by seed mortality from elevated temperature during fire. This general reduction contrasts with survival of temperatures greater than 100C by seeds of several species of mixed coniferous forests (Strickler and Edgerton 1976) and of chaparral (Keeley *et al.* 1985). The results presented here do not support the hypothesis that reduction was due to stimulation of germination by heat, as sometimes occurs in Douglas-fir forests (Gratkowski 1962), heathlands (Mallik and Gimingham 1985), chaparral (Keeley *et al.* 1985), and mixed coniferous forests of Sierra Nevada (Kauffman 1986).

Although this study tested several species with different growth forms and longevities, germination

responses were similar (Table 1): all species were killed at relatively low temperatures and none were stimulated by heat to germinate (Table 1). Other studies report a diversity of germination responses to heat treatments among species within a single ecosystem (Floyd 1966, Keeley *et al.* 1985, Mallik and Gimingham 1985, Bell *et al.* 1987). Species whose seeds are able to survive elevated temperatures or whose seeds are physically stimulated by heating are sometimes more prominent early in succession after disturbance (Floyd 1966, Keeley *et al.* 1985, Morgan and Neuenschwander 1988). Similarity of responses to elevated temperatures seen in this study, however, argues against fire as an agent favoring the seeds of one of the six study species over another.

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Epicormic Branching of California Black Oak: Effect of Stand and Tree Characteristics

Abstract

Young California black oak (*Quercus kelloggii* Newb.) stands usually require thinning to increase production of acorns and wood products, but epicormic branches, which yield no acorns and constitute a serious lumber degrade, often result. A crown thinning in 60-year-old hardwood stands on a south exposure at the Challenge Experimental Forest in the northern Sierra Nevada of California created basal areas that ranged from 20 to 35 m² per ha. Trees in a control and bordering small openings expanded the basal area range. In 1976 or 6 to 9 years after thinning, 2069 living and dead epicormic branches on 189 California black oak trees were observed. Statistically significant ($\alpha = 0.05$) predictors of epicormic branching were position in stand, cardinal direction of bole face, and bole segment—variables that generally affected epicormic branching on eastern species of deciduous oaks. Number of epicormic branches increased with decreasing stand density, proximity to openings, on south and east bole faces, and with increasing distance above the stump. These findings, together with silvicultural recommendations for enhancing crown development and lessening epicormic branching of California black oak, are discussed.

Introduction

Although native California hardwoods are virtually unmanaged and underutilized, the growing emphasis on ecosystem management and concern for a broad range of resource values is expected to bring about major changes. In California, black oak (*Quercus kelloggii* Newb.) exceeds all other native oak species in volume, distribution, and elevational range (McDonald 1969). Acorns are probably the most valuable current “yield” from California black oak (McDonald *et al.* 1983) with quality wood products a distant second.

To increase crown size and acorn production for wildlife management and to increase diameter and volume growth, managers need to thin oak stands (Tappeiner and McDonald 1980). But thinning usually results in excessive epicormic branching that in turn leads to serious lumber degrade. Epicormic branches are short (1 cm to 0.7 m long) branches that develop mostly below the live crown and produce few, if any, acorns. Such branches are responsible for more degrade in hardwood lumber than any other single agent (Kormanik and Brown 1967).

Because epicormic branches reduce wood quality, are visually unattractive, and produce no acorns, resource managers need information on how best to manage California black oak to lessen their presence. Our goal was to quantify a number of tree and stand characteristics and identify those that caused epicormic branching. Such knowledge should help managers decide on an ap-

propriate strategy for increasing stand growth, growing quality trees, and using conifer/hardwood mixtures to enhance both stand growth and bole quality.

Methods

Site and Stand

The study site, located about 42 km east of Oroville in the northern Sierra Nevada of California, is characterized by high site quality (black oak site index 18 m at 50 years [Powers 1972]), abundant annual precipitation (1727 mm), a warm climate (mean annual temperature 13°C), and a generally southern exposure.

The species composition and structure of the hardwood forest at Challenge is typical of that in the region and elsewhere in California and southwestern Oregon. In addition to California black oak, other species included tanoak (*Lithocarpus densiflorus* [Hook. & Arn.] Rehd.) and Pacific madrone (*Arbutus menziesii* Pursh), both of which seldom produce epicormic branches. The forest originated from a wildfire that killed most of the conifers, and the hardwoods to groundline. The hardwoods promptly sprouted. Hence the forest consisted of three hardwood species, was even-aged (about 60 years old when initially measured), and in general had a large number of trees per hectare. Within this general description, however, tree density was by no means uniform; rather it was high in places, less high in others, and even low occasionally. Small openings were scattered throughout.

Based on 0.1-ha plots located in relatively homogeneous stands, stocking of trees averaged 1628 per ha in the range of 5 to 41 cm d.b.h. (diameter at breast height) before thinning. Overall basal area was 47.7 m² per ha. Height of dominant and codominant trees averaged about 17 m. Average diameter growth rate of trees in unthinned stands was low—about 0.15 cm per year.

The epicormic branching investigation, part of a large stand- and tree-growth study, was conducted in eight stands. Seven of the eight stands, with an average basal area of 46.7 m² per ha, were randomly assigned a residual basal area in the range of 20 to 35 m² per ha. Residual basal area differed for each plot and was not replicated. The basal area of the eighth stand, the control, amounted to 48.0 m² per ha. "Crown" thinning was used to create open spaces into which crowns of retained trees could expand. Trees adjacent to small openings were designated "border" trees.

Sampling and Analysis

The development of epicormic branches was observed annually in the course of measuring trees and quantifying stand growth. In 1976 or 6 to 9 years after thinning, we counted epicormic branches on 189 black oaks: 93 in thinned plots (hereafter called "interior" trees), 71 in a control plot, and 25 on borders. These trees comprised all of the California black oaks 9.0 cm d.b.h. or larger in each plot.

The number of epicormic branches in all three categories totalled 2069: 83 percent living and 17 percent dead. Epicormic branches were counted on each California black oak bole, which was divided into cardinal directions. A bole "face," projected from the stem center, consisted of 45 degrees of bole circumference on each side of a cardinal direction. Sometimes a cluster of buds or short stubby branches were present. These were counted as one epicormic branch. Slender 5.4-m long aluminum rods, placed against the tree, defined each face. In addition, each bole face was divided into 2.5-m vertical segments. The bottom of the base segment began at 30 cm above mean ground line and extended to the base of the second segment. Concentrating on the two basal segments is appropriate because it is the basal portion that usually is the most valuable part of a hardwood tree (Trimble and Mendel 1969).

The total number of living and dead epicormic branches, relative to several tree and stand charac-

teristics, was analyzed by analysis of variance of transformed (square-root) values and linear and nonlinear regression (SAS Institute Inc. 1988).

Results and Discussion

Number of epicormic branches on California black oaks were all significantly ($\alpha = 0.05$) related to bole segment (just above stump or next highest), bole face (cardinal direction), and position in stand (border versus interior) (Table 1). Stand basal area was represented by the blocking factor, which was not truly replicated. Therefore no P value is presented for this term.

TABLE 1. Analysis of variance of epicormic branching¹ on California black oak boles, northern California.

Source of variation	Degrees of freedom	Sum of squares	F	P
Block	7	116.53	—	—
Border vs interior	1	54.68	23.63	0.0001
Crown class	2	8.89	1.92	0.1994
Border x crown class	2	0.60	0.13	0.8791
Error (a)	176	407.29	—	—
Bole face	3	40.20	30.66	0.0001
Bole segment	1	16.11	36.87	0.0001
Face x log	3	1.36	1.04	0.3756
Error (b)	1316	575.24	—	—

¹The dependent variable is the square-root of the number of epicormic branches. This transformation provided an analysis for which the residuals appear to be approximately normal.

For bole segment, the number of branches increased in general with distance from the stump to the base of the living crown. The mean number of epicormic branches (interior and border combined) was 4.4 branches for the base log and 6.7 for the second log, a highly significant difference ($P < 0.0001$) (Table 1).

Mean number of epicormic branches differed significantly by bole face (Table 1), which was analyzed further by Tukey tests ($\alpha = 0.05$). We found that (a) mean number of epicormic branches did not differ between south and east faces, (b) south and east faces had significantly more branches than north and west faces, and (c) mean number of epicormic branches was significantly greater on west than on north faces. The combination of south aspect and incident sunlight striking tree boles may account for these differences.

No relationship ($P = 0.15$) for epicormic branches among crown classes (59 dominant trees, 94 codominant trees, 36 intermediate trees) was found (Table 1). This was not surprising; number of epicormic branches apparently is a function of both crown configuration and bole surface area. We observed that smaller trees of the intermediate crown class do not have enough bole area to contain many dormant buds, which give rise to epicormic branches; medium-sized trees, most often of the codominant crown class, have enough bole area but narrow crowns and produce many epicormic branches; larger trees of the dominant crown class have adequate bole surface area and large crowns, but tend to have few epicormic branches.

Epicormic branching in California black oak also is related to decreased availability of site resources that results in an interesting postponement of mortality. While taking annual growth measurements, we noticed that overtopped, and hence smaller trees of the suppressed crown class, die from the top down and produce epicormic branches that also die from the top down. Although these trees usually succumb in 5 or 6 years after the top begins to die, epicormic branching prolongs life for an interval during which fire or logging could occur and kill the overstory. These trees then would sprout from the root crown. This form of epicormic branching took place on 10 trees in the control, but constituted 42 percent of the total number of epicormic branches produced there. Although unimportant silviculturally, this mortality postponement apparently constitutes an adaptive strategy to the fire environment in which this oak has evolved.

The amount of basal area that remains after thinning appears to influence the development of epicormic branches (Figure 1). However, because of the data collection techniques used in this study, it was not possible to statistically test the effect of basal area in the analysis of variance. Consequently, it was evaluated separately. To describe the relationship between number of epicormic branches and basal area, we applied a model using nonlinear regression and 189 trees:

$$N = \exp[\beta_0 + \beta_1 I + \beta_2 ba] \quad [1]$$

in which

$I = 1$ for border trees, 0 otherwise,

ba = breast height basal area (m^2/ha) of each stand, and

N = number of epicormic branches per tree.

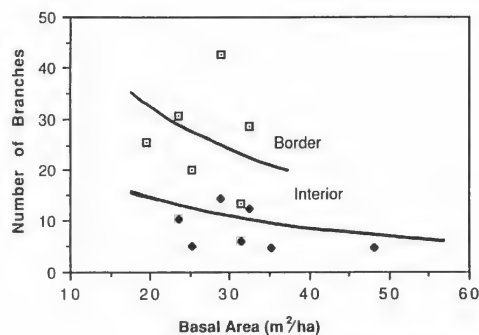


Figure 1. Number of epicormic branches for lower 4.9 m of tree bole relative to stand basal area for border and interior California black oak trees calculated by using equation [1].

The estimate for β_0 was 3.185 (asymptotic s.e. = 0.373); for β_1 , 0.841 (asymptotic s.e. = 0.162); for β_2 , -0.028 (asymptotic s.e. = 0.011). Because basal area is fixed for trees in any given stand, hypothesis testing of the basal area term in this regression is not recommended. The root mean square error was 11.7. This function indicates that a decrease in basal area of 10 m^2/ha , from 30 to 20 m^2/ha for example, would result in an expected increase of 7.8 epicormic branches per border tree and 3.4 branches per interior tree.

In this study, border trees averaged 19.2 more branches in the first two logs than interior trees. The reason for this can only be surmised, but it is logical that border trees have access to more site resources (soil moisture and light) than interior trees. After a disturbance that opens up a stand, these "extra" resources relative to the typical narrow crown of forest-grown trees, become manifest in epicormic branches. In a sense, these branches function as part of the crown for a short time and then die after the true crown develops.

Basal area is particularly important because the greater its value, the fewer the number of epicormic branches. This finding (Table 2), in conjunction with growth estimates reported earlier (McDonald 1980), allows the land manager to compare the thinning level with the expected growth and number of epicormic branches.

Study results show that the slightest reduction in the density of California black oak stands produces epicormic branches. Fully 94 percent of interior trees on thinned plots, but only 48 percent of trees in the control produced these branches. And the number of epicormic branches

TABLE 2. Relationship of basal area to predicted growth of stem volume and predicted number of epicormic branches on California black oak trees 10 years after thinning.

Basal area (m ² /ha)	Predicted volume growth per interior tree over 10-year period	Predicted number of epicormic branches for lower 4.9 m of tree bole	
	(m ³)	Interior	Border
19.5	0.113 ¹	—	32.5
23.4	0.102	12.6	29.1
25.3	0.097	12.0	27.5
28.7	0.087	10.9	25.1
31.2	0.080	10.2	23.4
32.4	0.077	9.8	22.6
35.1	0.070	9.1	—
48.0	0.034	6.4	—

¹Values smoothed by regression: volume growth = 0.167-0.0028 basal area, root mean square error = 0.0218

can be large—up to 86 per lower 4.9 m of bole on border trees. The paradox is that while thinning promotes fast-growing trees, it also causes large numbers of epicormic branches to develop. Thinning also is desirable for development of large crowns capable of producing large and frequent acorn crops, vital to many species of wildlife.

Of particular note is that the tree and stand characteristics that cause epicormic branching on black oaks in California are the same characteristics in general that lead to epicormic branching on oaks in the eastern United States (Ward 1966, Carl H. Tubbs, pers. comm.). This similarity is of ecological interest, given the large differences in environments (season of precipitation, frequency and intensity of fire) between California and the eastern United States.

Management Considerations

Study results suggest three possible silvicultural considerations to lessen epicormic branching in similar and mixed stands, and to increase acorn and wood product yields. The first two involve a thinning regime and the second deals with compartment size.

The interrelationship of stand density, tree vigor, and crown size denoted in this study suggests that a series of thinnings may enhance both acorn and wood production. The key is that vigorous trees have better developed crowns and produce fewer epicormic branches. After the first thinning, some degree of epicormic branching probably is inevitable. However, more site resources would be available to the remaining trees, and their vigor and crown size would increase. Fewer epicormic branches and more acorns should be produced in ensuing thinnings. Consequently, the manager might wish to thin lightly at first and follow with heavier thinnings.

In naturally-occurring mixed hardwood/conifer stands, which are common at mid-elevations in southern Oregon and California, California black oak most often originates as root-crown sprouts and the pines and firs as seedlings. With careful and innovative stand manipulation, each species can aid the other. Partial shade from the oaks can lessen environmental stress for the conifers, especially when seedlings, and their shade, when older, can shield black oak boles and lessen epicormic branching.

Because California black oaks on borders produce a disproportionately large number of epicormic branches relative to interior trees, the proportion of trees near the border should be minimized by managing the species in larger compartments, thereby reducing the amount of edge.

Sudden exposure of California black oak trees to increased amounts of site resources almost always leads to epicormic branching and a degrade in bole quality. However, the magnitude of branching and the environmental factors that cause it may vary with site quality, tree size, and the amount of sunlight striking the tree bole. This study presents results for trees of one age (but of various sizes) on one exposure, and provides initial knowledge for at least part of the epicormic branching phenomenon. A second study, soon to be reported, will examine epicormic branching relationships for older trees on a different exposure.

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C. David McIntire, Department of Botany & Plant Pathology, Oregon State University, Corvallis, Oregon 97331-2902

Harry K. Phinney (deceased), Department of Botany & Plant Pathology, Oregon State University, Corvallis, Oregon 97331-2902

Gary L. Larson, National Biological Survey, Cooperative Park Studies Unit, College of Forestry, Oregon State University, Corvallis, Oregon 97331-5703

and

Mark Buktenica, National Park Service, Pacific Northwest Region, Crater Lake National Park, Crater Lake, Oregon 97604-0007

Vertical Distribution of a Deep-water Moss and Associated Epiphytes in Crater Lake, Oregon

Abstract

A one-person submersible was used to examine the vertical distribution of the deep-water moss *Drepanocladus aduncus* (Hedw.) Warnst in Crater Lake (Oregon). Living specimens were found attached to sediment and rocks at depths between 25 m and 140 m. Dense beds of the moss were observed at depths between 30 m and 80 m, a region that corresponded roughly to the zone of maximum primary production by phytoplankton. The moss population supported a diverse assemblage of epiphytic algae, of which the most abundant genera included *Cladophora*, *Oedogonium*, *Rhizoclonium*, *Tribonema*, *Vaucheria*, and the diatoms *Cocconeis*, *Cymbella*, *Epithemia*, *Fragilaria*, *Gomphonema*, *Melosira*, *Navicula*, and *Synedra*. Chemical and physical data supported the hypothesis that the lower limit of distribution of the moss is determined by light limitation, whereas the upper limit is related to the availability of nutrients, particularly nitrate-nitrogen and trace elements. Deep-water videotapes of the moss population indicated that *D. aduncus* with its epiphytic algae was abundant enough in regions associated with the metalimnion and upper hypolimnion to have a potential influence on the nutrient dynamics of the Crater Lake ecosystem. Although the maximum depth at which living bryophytes occur in Crater Lake is similar to that found for Lake Tahoe, conditions in Lake Tahoe allow the growth and survival of a much more diverse assemblage of bryophytes and charophytes than is present in Crater Lake.

Introduction

Relatively little information is available on the distribution and ecological significance of deep-water bryophytes and algae in the freshwater ecosystems of the world. Sparse distributional records clearly indicate that some species of mosses, liverworts, and algae can survive in lakes at depths considerably greater than 15 m, a depth which is usually considered to be the lower limit for aquatic angiosperms (Hutchinson 1975). Frantz and Cordone (1967) identified ten species of mosses, two species of liverworts, and six species of algae in samples taken from depths between 7 m and 124 m in Lake Tahoe, an ultra-oligotrophic lake with high transparency and low primary productivity. In this study, *Leptodictyum riparium* (Hedw.) Warnst., the most abundant and widely distributed moss, was collected at depths ranging from 30 m to 124 m, whereas the liverwort *Blepharostoma arachnoideum* Howe was found between depths of 60 m and 122 m. In addition, the absence of the genus *Drepanocladus* from the moss samples was noted.

Crater Lake (Oregon) also is classified as an ultra-oligotrophic lake and has limnological con-

ditions similar to those reported for Lake Tahoe (G. Larson *et al.* 1993a). Although early biological studies of the benthic flora and fauna of Crater Lake were limited by the sampling methods and equipment available at the time, both Brode (1938) and Hasler (1938) found that a deep-water moss was present in dredge samples obtained from depths as great as 120 m below the water surface. A study of the Crater Lake ecosystem between 1982 and 1988 (Drake *et al.* 1990) stimulated considerable interest in this organism, because of its apparent potential to generate large biomasses at depths of 30 m or more below the water surface. However, relationships between the deep-water moss, with its assemblage of epiphytic algae, and the nutrient dynamics and bioenergetics of the Crater Lake ecosystem remain unknown.

In August 1989 a series of deep-water dives were made at selected locations in Crater Lake using *Deep Rover*, a one-person submersible. These dives were designed to: (1) identify the magnitude and characteristics of hydrothermal inputs to the deep lake (Collier *et al.* 1991); (2) obtain geological specimens for interpretation; and (3) investigate

the taxonomic composition of deep-water benthic communities in the lake. The presence of the submersible provided a unique opportunity to examine the distribution of a deep-water moss and its associated epiphytes in one of the deepest and clearest lakes in the world. The objectives of the study reported in this paper were to establish the vertical distributional boundaries for this moss at selected study sites and to describe its epiphytic algal flora. In addition, distributional patterns in the benthic flora were related to chemical, physical and biological data obtained from the water column of the lake between 1982 and 1990 (G. Larson 1985, 1987, 1989, 1991) and to distributional records for other lakes.

Study Area

Crater Lake is located in south-central Oregon at 42°56'N and 122°06'W. The lake is contained by the caldera of Mount Mazama, which formed after a climactic eruption and collapse, approximately 6,800 years ago (Bacon 1983). The catchment area is small (15 km²) and consists of the steep walls of the caldera and Wizard Island, a small, exposed cinder cone. Crater Lake is the deepest lake in the United States and the seventh deepest lake in the world, with a maximum depth of 589 m, a surface area of 53.2 km², and a volume of about 16 km³ (Byrne 1965, Phillips and Van Denburgh 1968). Inputs of water and nutrients to the lake are confined to precipitation and atmospheric fall-out, surface run-off and snow-melt from inside the caldera, and introductions from small springs and streams within the caldera (Phillips and Van Denburgh 1968). In general, the lake has very low concentrations of nutrients, a high Secchi disk transparency (usually between 28 m and 33 m), low rates of primary production in the water column, and summer primary production and chlorophyll maxima at depths between 40 m and 80 m and between 100 m and 140 m, respectively (G. Larson 1985, 1987, 1989, 1991; D. Larson *et al.* 1987).

A recent study of the physical limnology of Crater Lake (McManus 1992) indicates that the annual vertical exchange of surface water with water from the deep lake (>200 m) occurs during the early winter and to some extent during the late spring. However, this mixing process is not complete, as the deep lake does not reach atmospheric saturation with respect to dissolved oxygen at any

time during the year. In the winter and spring, the water mass circulates to a depth between 200 m and 250 m. The temperature of the lake near the water surface increases in late spring or early summer, at which time the water column begins to exhibit the early stages of thermal stratification. In some years thermal stratification is evident as early as June, whereas in other years the process is not complete until September. During the period from 1982 through 1990, the epilimnion varied between 5 m and 20 m in depth, depending on the month of the year, and was deepest in September; the corresponding depth range for the metalimnion usually extended from the lower limit of the epilimnion to 80 m below the water surface (G. Larson and McIntire 1993). The annual maximum surface water temperature observed during the summer months between 1982 and 1990 ranged from 14.6° C (1987) to 19.2° C (1989).

Sampling and Laboratory Methods

The dives that provided samples of biological material from Crater Lake were made on the northwest side of the lake near Llaio Rock, on the northeast and southeast sides off Palisades Point and Sentinel Rock, south of Wizard Island, and in the deep water of the northeast basin (Figure 1). Dives 219, 221, 225 and 227 were designed to locate and collect biological specimens from deep-water benthic communities. In addition, biological samples were obtained from rocks collected during three dives for the U. S. Geologic Survey (dives 210, 212 and 214) and one dive designed for hydrothermal exploration (dive 228). Along with material collected with the submersible, the moss found in dredge samples taken near Wizard Island on July 25-27, 1989 also was included in the study. The microscopical examination of biological specimens was facilitated by a set of videotapes obtained during each dive.

Moss samples collected during the deep-water dives were removed from the substrate by controlling two manipulators mounted on the front of the submersible. A metal furniture clamp with a short piece of rope at one end was held open by a manipulator and subsequently dropped into the moss bed. The clamp with the trapped sample of moss was retrieved by the manipulator and transferred to a wire basket located in front of the submersible. During the geological dives rock samples with attached moss also were collected with the

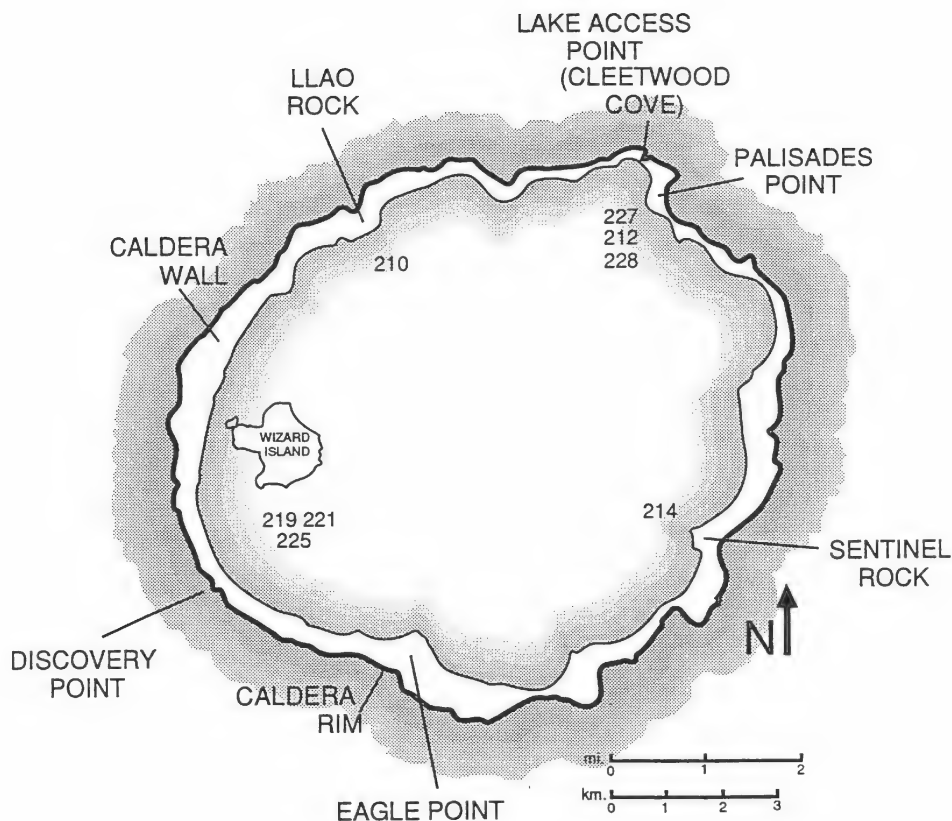


Figure 1. Map of Crater Lake indicating the location of deep-water dives that provided samples of biological material in August 1989.

manipulators. After each dive, the samples were sorted, refrigerated and returned to the laboratory for examination. Representative specimens from each moss collection were examined with a compound microscope at magnifications ranging from 100X to 1000X. A list of dominant epiphytes and a subjective evaluation of the condition of the moss and associated algae were recorded for each specimen. In addition, epiphytic diatoms were mounted in Cumarone resin (Holmes *et al.* 1981) after sub-samples of each moss collection were boiled in nitric acid. These permanent mounts were used to compile a list of dominant epiphytic diatom species for Crater Lake. Specimens of the deep-water moss were deposited in the Oregon State University Herbarium (OSC) and in the natural history collection at Crater Lake National Park. The dia-

tom samples are still under study by the senior author and will eventually be deposited in the Diatom Herbarium at the Philadelphia Academy of Natural Sciences (ANSP).

All chemical and physical data were recorded for the water column in the deepest basin of Crater Lake, approximately 3 km south of Cleetwood Cove (Figure 1). Patterns of circulation in the lake (McManus 1992) indicated that chemical and physical data from this location were representative of patterns in the water column in most areas of the lake down to a depth of 200 m, the maximum depth of complete mixing on an annual basis. Water temperature measurements were made with a Sea Bird conductivity-temperature-depth probe (Model SB E19) in January, June, July, August, and September 1990. The depth at which

irradiance was 1% of the surface intensity was measured with a Kahl Submarine Photometer in the spring, summer, and fall at irregular intervals from 1980 to 1989. Concentrations of nitrate-nitrogen in the water column were determined by a series of measurements made between 1982 and 1990. Water samples for these analyses were processed with a Technicon Autoanalyzer at the Cooperative Chemical Analytical Laboratory, Oregon State University.

Results and Discussion

Taxonomy

The history of the discovery and identification of the moss growing deep in Crater Lake has been reviewed recently by Phinney (1989). This review also included a detailed morphological description of specimens collected by Sylvia Earle (California Academy of Sciences) during one of the earlier submersible dives in the summer of 1988. Moss samples from deep-water locations in Crater Lake (depths > 20 m) have been identified by ecologists and taxonomists as *Fontinalis* and *Drepanocladus* (Hasler 1938), *Fontinalis howellii* Ren. & Card. (W. Welch 1935, unpublished), *Fontinalis* (Brode 1938), *Drepanocladus fluitans* (Hedw.) Warnst. (F. Drouet 1954, unpublished), *D. fluitans* (J. R. Rowley 1952, unpublished), and *D. aduncus* (Hedw.) Warnst. (E. Lawton 1965, unpublished). Unfortunately, most of the earlier samples were lost, and it was not possible to establish whether or not specimens examined by these individuals represented the same species collected in 1988 and 1989. Moss samples obtained south of Wizard Island during dive 219 in August 1989 were identified by D. Norris (Department of Botany and Plant Pathology, Oregon State University) as *D. aduncus*, an interpretation that was consistent with Lawton's identification in 1965. In the following discussion, we refer to the deep-water moss collected from Crater Lake in 1989 as *D. aduncus*.

The Vertical Distribution of *Drepanocladus aduncus*

Although the lake exhibited great clarity and low primary productivity in the water column, benthic communities of moss and epiphytic algae were dense and diverse in certain areas in contact with the metalimnion and upper part of the hypolimnion. These communities were particularly well-

developed in a region south of Wizard Island, i.e., the locations of dives 219, 221 and 225 (Figure 1).

The vertical distribution of *Drepanocladus aduncus* in Crater Lake, as revealed by the study in 1989, is summarized in Table 1. During the biological dives (219, 221, 225, and 227) moss samples were collected at selected locations from the upper limit of distribution to a depth where only detrital specimens were observed. The upper limit of distribution of *D. aduncus* also was explored during geological dive 212 near Palisades Point. From these observations, it was apparent that *D. aduncus* occurred at depths below about 25 m, as no specimens were collected between this depth and the water surface. Dense beds of the moss were observed and recorded on videotapes by the submersible pilot (M. Buktenica) at depths between 30 m and 80 m, a region corresponding roughly to the zone of maximum primary production by phytoplankton in the water column (D. Larson *et al.* 1987, G. Larson 1985, 1987, 1989, 1991). The lower boundary of active growth was harder to establish because of uncertainties about the physiological state of samples obtained at depths below 100 m. The deepest collection of moss in which the plants were observed to be attached and in good condition was taken from a rock at a depth of 118 m. All specimens collected below this depth were obtained from sediment and consisted of dead cells, or in one case (dive 214 from 223 m), material with both living and dead cells. However, the submersible pilot reported seeing living material growing on rock near Palisades Point at a depth of 140 m. This observation and two other observations at 125 m and 135 m near Wizard Island were recorded on videotape. Therefore, best estimates of the upper and lower depth limits of distribution for *D. aduncus* in the living condition were 25 m and somewhere between 118 m and 140 m, respectively. Nevertheless, all specimens collected from depths below 120 m, including those with a few living cells, were probably part of detrital inputs which apparently can cascade down the steep walls of the caldera from the zone of maximum population biomass. It is not surprising that living cells were found in specimens taken from below 200 m, because metabolic rates were undoubtedly low at such depths where the water temperature remained below 4° C throughout the year (Figure 2).

The lower distributional limit of *Drepanocladus aduncus* in Crater Lake may be determined by the

TABLE 1. Summary of the depths at which specimens of *Drepanocladus aduncus* were obtained from Crater Lake in August 1989. The comments relate to laboratory observations of the specimens and to field observations by the submersible pilot. The term "detritus" refers to moss specimens with no observed living cells. The dives are the same as those illustrated in Figure 1.

Dive	Depth	Substrate	Comments
219	26 m	sediment	living, with a diversity of epiphytes
219	29 m	sediment	in good condition
219	30 m	sediment	from dense bed
219	38 m	sediment	from dense bed
219	46 m	sediment	in good condition
**	46 m	sediment	in good condition
**	48 m	sediment	epiphytes abundant
219	53 m	sediment	from dense bed
210	59 m	rock	old plants, sparse
219	62 m	sediment	from dense bed
225	70 m	sediment	in good condition with epiphytes
227	70 m	sediment	some living and some dead plants
225	78 m	sediment	95% living and 5% dead
219	80 m	sediment	brownish, detrital material
212	83 m	rock	in good condition
214	84 m	rock	plants in good condition
210	90 m	sediment	no comment
225	90 m	sediment	detrital
227	91 m	sediment	in good condition
214	92 m	sediment	in living condition
212	94 m	rock	with many epiphytes
**	100 m	sediment	with many epiphytes on tips of plants
219	101 m	sediment	detrital
212	116 m	rock	plants with abundant lateral rhizoids
214	118 m	rock	in good condition with epiphytes
219	121 m	rock	cells with no living contents
227	124 m	sediment	detrital
219	155 m	sediment	detrital
214	223 m	sediment	with some living and some dead cells
214	229 m	sediment	detrital
227	529 m	sediment	detrital
227	536 m	sediment	detrital
227	545 m	sediment	detrital

** Record from dredge samples obtained July 25-27, 1989

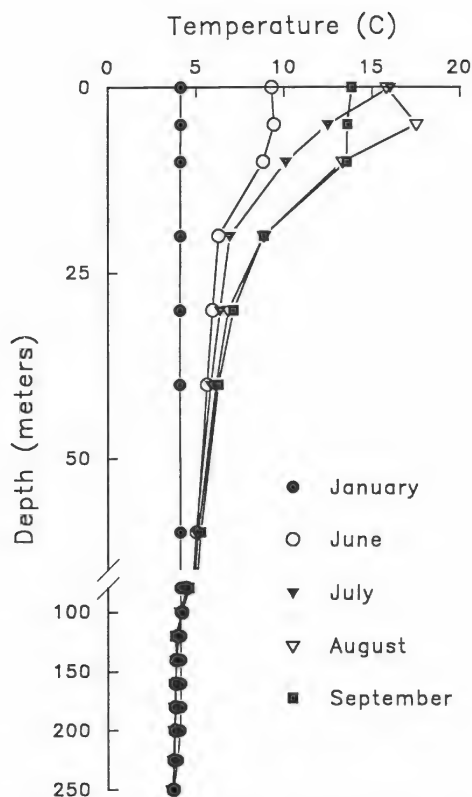


Figure 2. Temperature profiles in Crater Lake obtained in January, June, July, August and September 1990.

depth of effective light penetration, because many other physical and chemical variables (e.g., temperature and nutrient concentrations) do not exhibit conspicuous changes in value between depths of 80 m and 150 m. The depth at which irradiance is approximately 1% of the intensity at the lake surface is usually between 80 m and 100 m (Figure 3), a range that corresponds closely to the lower limit of the maximum density of *D. aduncus*. Frantz and Cordone (1967) reported the occurrence of *Fontinalis nitida* Lindb. & Arn. at a maximum depth of 122 m in Lake Tahoe. The irradiance at this depth was about 0.13% of the intensity at the surface. In Crater Lake the corresponding irradiance at 120 m was approximately 0.1% of the surface intensity when the 1% depth was at 80 m. Therefore, we conclude that the irradiances at the lower distributional limit for mosses in Lake Tahoe and Crater Lake are similar.

Some hypotheses accounting for the upper distributional limit of *D. aduncus* in Crater Lake include: (1) distribution is limited to the metalimnion and upper hypolimnion because of warm summer temperatures in the epilimnion (Figure 2); (2) population growth is inhibited in the upper 25 m of the water column by high irradiance; (3) the moss is excluded from the upper 25 m of the water column by grazing activities of aquatic animals; (4) substrate characteristics above the depth of 25 m are unsuitable for the establishment and growth of bryophytes; and (5) upper distribution is determined by nutrient limitation, particularly during thermal stratification in the summer. *Drepanocladus aduncus* has been found in boggy habitats, in swamps and marshes, and submerged and emergent in shallow water over a wide geographical range in the eastern and western United States (Crum and Anderson 1981). In addition, Wynne (1944) reported the occurrence of *D. aduncus* var. *kneiffii* (B.S.G.) Mönk. at a depth of 10.7 m in Linn County, Oregon (lake not specified). Consequently, distributional records are inconsistent with the temperature and light inhibition hypotheses, unless the population in Crater Lake represents a distinct ecotype with different physiological requirements than other varieties of this species. Coffey and Clayton (1988) found that the lower distribution of bryophytes in Lake Wanaka (New Zealand) was determined by the grazing activities of a crayfish (*Paraneohpops*). Although a variety of benthic invertebrates were collected in Crater Lake between the shoreline and depths below 120 m (Wiseman *et al.* 1993), there are no data to suggest that grazing is more intense in the upper 25 m of the water column than at greater depths. Furthermore, local patches of green filamentous algae, usually *Zygnema*, *Mougeotia*, *Ulothrix*, or *Cladophora*, and diatoms often are observed in the upper 5 m of the littoral zone of the lake near spring inlets and near suspected sources of ground water around Wizard Island, possibly indicating that benthic grazing has relatively little impact on autotrophic assemblages in the shallow-water regions of the lake. Frantz and Cordone (1967) reported that deep-water hydrophytes in Lake Tahoe were restricted to areas where the substrate consisted of silt-size particles, and that densities were sparse at depths less than 30 m where the substrate was composed of sand and gravel. Although it is not possible to disregard the effects of substrate type on the distribution of *D. aduncus* in Crater Lake,

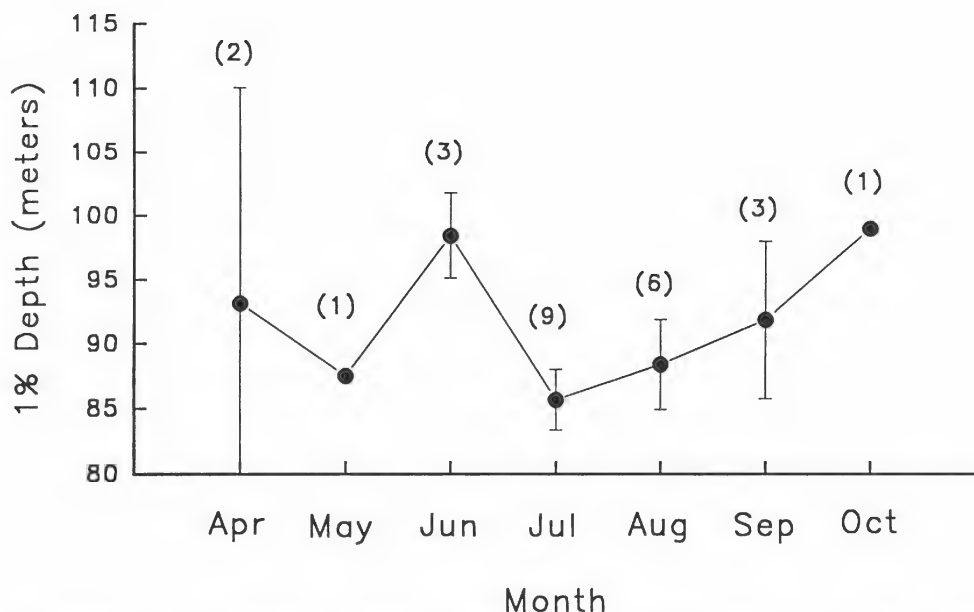


Figure 3. Depth at which the availability of light energy is 1% of the irradiance at the water surface. Error bars indicate the standard error of the mean, and the numbers above each bar are the number of observations recorded for each month.

videotapes of the dives failed to disclose any obvious discontinuities in substrate characteristics in the region of the upper limit of distribution, i.e., at a depth of about 25 m.

All chemical data obtained for Crater Lake between 1983 and 1990 (G. Larson 1985, 1987, 1989, 1991) indicated that the concentration of nitrate-nitrogen was extremely low in the upper 200 m of the water column, often less than $1 \mu\text{g/l}$ (Figure 4). Preliminary bioassays with a standard test organism (*Selenastrum*) demonstrated that the addition of nitrate in combination with a source of iron and other trace elements to samples of Crater Lake water greatly enhanced the capacity of the water to produce algal biomass (Groeger and Tietjen 1993). Moreover, calculations from sediment trap data suggested that between 85% and 90% of the nitrogen in Crater Lake was recycled, and that upwelling events in winter and spring from the deep lake (depths > 200 m) provided 80% to 90% of the total nitrogen input to the euphotic zone (Dymond and Collier 1993). An examination of benthic communities at locations where small springs enter the lake also revealed algal biomasses that were large enough to remove some of the

meager nutrient inputs from the caldera walls during periods of thermal stratification. Consequently, the input of nitrogen and other nutrients into the epilimnion was very low during the summer months when this layer was sealed off from recycling processes that occurred at depths below 20 m. G. Larson *et al.* (1993b) found that most zooplankton taxa in Crater Lake reached maximum densities in either the metalimnion or upper hypolimnion (i.e., between depths of 40 m and 120 m) during summer months and had relatively low densities in the epilimnion. Results of this study and a nitrogen budget derived from the sediment trap data (Dymond and Collier 1993) supported the hypothesis that nutrient recycling by the diverse assemblage of zooplankton below the epilimnion accounted, in part, for the observed primary production maximum in the water column between the depths of 40 m and 80 m. Therefore, enough recycling apparently occurs in the euphotic zone below the epilimnion to support the *Drepanocladus* population, whereas nutrient impoverishment above 25 m during the summer months may be unfavorable for the establishment of this moss at depths corresponding to the epilimnion.

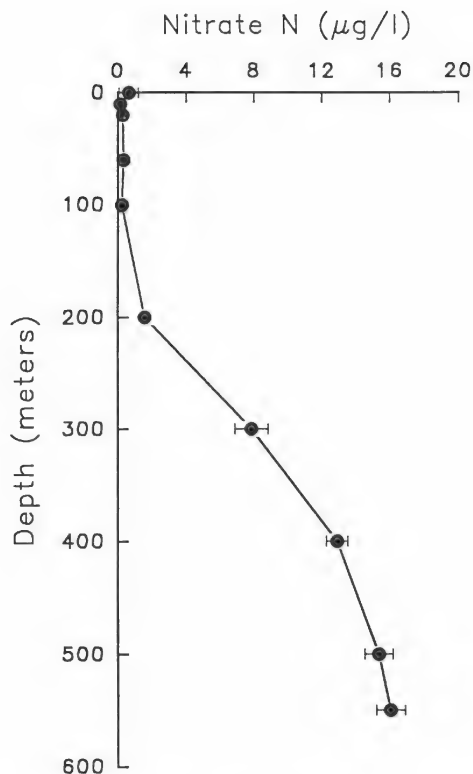


Figure 4. Concentrations of nitrate-nitrogen in the water column of Crater Lake. Data points are mean values for all measurements made between 1982 and 1990. Error bars represent the standard error of the mean.

Epiphytic Algae

The assemblages of algae attached to *Drepanocladus aduncus* in Crater Lake were diverse and often consisted of representatives of the Bacillariophyceae, Chlorophyta, Cyanophyta (cyanobacteria), and Xanthophyceae. Filamentous chlorophytes (e.g., species of *Cladophora*, *Oedogonium*, and *Rhizoclonium*) were abundant epiphytes between depths of 25 m and 80 m (Table 2). *Oedogonium* was found on one detrital moss sample from a depth of 223 m, the location of the deepest sample with living chlorophytes. Filamentous chlorophytes often exhibited a conspicuous flora of epiphytic diatoms, particularly *Melosira undulata* (Ehr.) Kütz. and species of *Cymbella*, *Epithemia*, and *Gomphonema*. Filamentous xanthophytes were abundant epiphytes on *D. aduncus* be-

tween depths of 40 m and 120 m (Table 2). *Tribonema bombycinum* (C. A. Ag.) Derbés & Solier and a species of *Vaucheria* were the most abundant of these taxa, the latter taxon often supporting a prominent assemblage of stalked and filamentous epiphytic diatoms. Of all the observed filamentous chlorophytes and xanthophytes, *Vaucheria* apparently had the greatest tolerance for low light levels, as living cells were found attached to detrital moss samples collected at depths below 200 m. Frantz and Cordone (1967) reported the presence of *Cladophora glomerata* (Linn.) Kütz. and *Vaucheria* in Lake Tahoe at depths of 125 m and 110 m, respectively, the deepest specimens of algae found during that study. *Nostoc*, the most abundant representative of the cyanobacteria in Crater Lake, was associated with *Drepanocladus* down to a depth of 118 m.

Sovereign (1958) published a list of 66 diatom taxa identified in four benthic samples from the littoral zone around Wizard Island. The most common epiphytic diatoms found in the August 1989 samples were *Cocconeis*, *Cymbella*, *Epithemia*, *Fragilaria*, *Gomphonema*, *Melosira*, *Navicula*, and *Rhoicosphenia*, genera that were often abundant at depths down to 120 m. A more detailed analysis of the epiphytic diatom flora revealed a diverse assemblage of species which included many of the same taxa found growing on rock or sediment by Sovereign in 1958. For example, one moss sample collected during dive 219 from a depth of 29 m contained 41 abundant diatom species and varieties of species (Table 3) and many rarer taxa. Of particular interest was *Melosira undulata*, a filamentous centric diatom that attached to moss tissue and other surfaces by a series of gelatinous strands which were extruded through rows of pores in the cell wall. Living cells of this relatively large species were found growing on both living and detrital moss at depths down to 223 m. This taxon has a relatively broad geographical distribution and is known to occur in the benthos of other deep-water lakes, e.g., Lake Michigan (Stoermer and Yang 1969) and Lake Tahoe (Mahood *et al.* 1984).

Ecological Significance

Although the optical properties and primary productivity of Crater Lake and Lake Tahoe are similar, characteristics of the deep-water benthic communities in the two systems differ with respect

TABLE 2. Summary of the distribution of benthic algae (other than diatoms) collected during the deep-water dives listed in Table 1. The letter L indicates that the alga was observed in living condition, whereas D indicates that detrital cells were abundant in at least one sample from the corresponding depth range.

Taxon	Depth Range (Meters)				
	20-40	40-80	80-120	120-200	200-560
Chlorophyta:					
<i>Bulbochaete</i>	L	L	L		
<i>Chaetosphaeridium globosum</i>	L				
<i>Cladophora crispata</i>			L		
<i>Cosmarium</i>	L				
<i>Microspora stagnorum</i>		L			
<i>Microsterias</i>		L			
<i>Mougeotia</i>	L	L	L		
<i>Oedogonium</i>	L	L	L		L
<i>Palmodictyon viride</i>		L			
<i>Pediastrum boryanum</i>	L				
<i>Pleurotaenium</i>	L				
<i>Rhizoclonium heiroglyphicum</i>		L	L		
<i>Sirogonium</i>	L				
<i>Spirogyra</i>	L	L	L		
<i>Staurastrum</i>	L				
<i>Zygnema</i>	L	L	L		
Cyanobacteria:					
<i>Nostoc</i>	L	L	L	L	
Xanthophyceae:					
<i>Ophiocytium</i>		L			
<i>Tribonema bombycinum</i>	L	L,D	L,D		L
<i>Tribonema tenerrima</i>		L	L		
<i>Vaucheria</i>		L,D	L,D		L,D
Euglenophyta:					
<i>Phacus orbicularis</i>	L				

to species composition and diversity of bryophytes. Whereas some of the differences noted between the two lakes may be related to inappropriate taxonomic designations, there is no doubt that species diversity of deep-water macrophytes in Lake Tahoe is considerably greater than in Crater Lake. Samples obtained in 1988 and 1989 from Crater Lake indicate that there is only one dominant bryophyte (*Drepanocladus aduncus*) and a conspicuous absence of the genus *Chara* (Charophyta). In contrast, conditions in Lake Tahoe apparently allow the growth and survival of a much more diverse assemblage of bryophytes and charophytes. Moreover, the failure to find representatives of the genus *Drepanocladus* in Lake Tahoe suggests that this genus may be more competitive in deep water when extreme physical conditions restrict habitat

diversity and the distribution of other taxa. In particular, the relatively small surface area to depth ratio and the steep caldera walls of Crater Lake generate a broad region of nutrient impoverishment well below the euphotic zone and below the depth of the chlorophyll maximum in the water column (ca. 120 m).

The distribution and abundance of *D. aduncus* is not only of interest from a taxonomic and autecological point of view, but also from a synecological perspective, because of the potential impact of this organism on nutrient supply and recycling in the water column. Dymond and Collier (1993) found that fluxes of nitrogen which entered the euphotic zone of Crater Lake by deep lake upwelling, precipitation, and runoff were 2 to 10 times larger than nitrogen fluxes measured in sediment traps

TABLE 3. List of 41 common diatom species and varieties associated with a sample of *Drepanocladus aduncus* collected during dive 219 from a depth of 29 m.

<i>Achnanthes calcar</i> Cl.	<i>Eunotia pectinalis</i> var. <i>minor</i> (Kütz.) Rabh.
<i>Achnanthes clevei</i> Grun.	<i>Fragilaria brevistriata</i> Grun.
<i>Achnanthes lanceolata</i> (Bréb.) Grun.,	<i>Fragilaria construens</i> (Ehr.) Grun.
<i>Achnanthes minutissima</i> Kütz.	<i>Fragilaria construens</i> var. <i>ventor</i> (Ehr.) Grun.
<i>Achnanthes peragalli</i> Brun. & Hérib.	<i>Fragilaria pinnata</i> Ehr.
<i>Amphora ovalis</i> Kütz.	<i>Fragilaria pinnata</i> var. <i>trigona</i> (Brun & Hérib.) Hust.
<i>Amphora ovalis</i> var. <i>pediculus</i> Kütz.	<i>Fragilaria virescens</i> Ralfs
<i>Caloneis hyalina</i> Hust.	<i>Gomphonema ericense</i> Grun.
<i>Cocconeis klamathensis</i> Sov.	<i>Gomphonema parvulum</i> (Kütz.) Rabh.
<i>Cocconeis pediculus</i> Ehr.	<i>Gomphonema</i> cf. <i>manubrium</i> Fricke
<i>Cocconeis placentula</i> var. <i>euglypta</i> (Ehr.) Cl.	<i>Melosira undulata</i> (Ehr.) Kütz.
<i>Cocconeis rugosa</i> Sov.	<i>Navicula cryptocephala</i> var. <i>veneta</i> (Kütz.) Rabh.
<i>Cymbella cistula</i> (Hempr.) Grun.	<i>Navicula pupula</i> Kütz.
<i>Cymbella mexicana</i> (Ehr.) Cl.	<i>Navicula radiosa</i> Kütz.
<i>Cymbella minuta</i> Hilse ex. Rabh.	<i>Navicula viridula</i> Kütz.
<i>Cymbella muelleri</i> Hust.	<i>Nitzschia oregona</i> Sov.
<i>Diatomella balfouriana</i> Grev.	<i>Rhoicosphenia curvata</i> (Kütz.) Grun.
<i>Diploneis elliptical</i> (Kütz.) Cl.	<i>Rhoicosphenia curvata</i> var. <i>major</i> Cl.
<i>Epithemia adnata</i> (Kütz.) Breb.	<i>Synedra mazamaensis</i> Sov.
<i>Epithemia sores</i> Kütz.	<i>Synedra parasitica</i> (W. Sm.) Hust.
<i>Epithemia turgida</i> (Ehr.) Kütz.	

deployed in the central region of the lake. Consequently, they hypothesized that biological productivity was relatively high near the caldera walls and in the shallow water regions around Wizard Island, and that detritus from these regions of high benthic primary production was transferred from the lake margins to the deep lake by winter storms and mixing events. Results of our study of *D. aduncus* and its associated epiphytes provided direct observations of moss and algae that were abundant enough to account for the translocation of some organic materials and nutrients to the deep lake. Although these assemblages exhibited high biomasses in some of the study areas, their relative importance in an energy and nutrient budget for the entire lake is unknown. Therefore, future investigations of the deep-water moss population in Crater Lake should include studies that emphasize bioenergetics, nutrient dynamics, and the couplings between benthic autotrophs and the planktonic assemblages in the water column.

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P. A. McDaniel, Soil Science Division, University of Idaho, Moscow, Idaho 83844-2339

K. E. Houston, U.S. Forest Service, Cody, Wyoming 82414-2140

M. A. Fosberg, Soil Science Division, University of Idaho, Moscow, Idaho 83844-2339

and

A. L. Falen, Soil Science Division, University of Idaho, Moscow, Idaho 83844-2339

Soil-Plant Community Relationships in the Selkirk Mountains of Northern Idaho

Abstract

Soils and the native plant communities they support often exhibit a strong mutual dependence within geographically similar areas. In mid- to high-elevation forests of northern Idaho, volcanic ash is an important soil parent material and has had a major impact on soil properties and the distribution of vegetation. As a result, there are several well-expressed soil-plant community type associations within this region. This study compares the properties and classification of soils and plant communities along a south-facing elevational gradient in the Selkirk Mountains of northern Idaho. Cold, moist soils of the higher elevations, corresponding to the *Abies lasiocarpa* (subalpine fir) series, are strongly influenced by volcanic ash. These soils have undergone intense podzolization and are classified as Spodosols. The intermediate moisture and temperature conditions associated with the middle elevations support plant communities of the *Tsuga heterophylla* (western hemlock) series. Associated soils exhibit progressively less influence of volcanic ash with decreasing elevation. Accordingly, soils of the upper end of the western hemlock zone are classified as Andisols and those of the lower end are classified as intergrades to the Andisols. At relatively low elevations, the warmest and driest soils of the climatic gradient support communities of the *Pseudotsuga menziesii* (Douglas-fir) series. These soils contain little or no volcanic ash and are classified as non-andic Inceptisols and Entisols. Results from this study indicate that increased sensitivity of Soil Taxonomy to ash-influenced soils helps distinguish several of the important soil-vegetation interactions that have been operative in this region. As a result, interrelationships between soils, their classification, and associated plant communities can be clearly demonstrated for these and, presumably, similar forested ecosystems of the Pacific Northwest.

Introduction

Interrelationships between soils and the vegetation they support are often observed by field soil scientists and plant ecologists. In recognizing the close relationship between plant communities and soil-forming processes, Jenny (1941) included organisms (primarily vegetation) as one of the five soil-forming factors in his widely used model of soil genesis. Major (1951) used a similar set of independent variables to define a climax plant community. Thus, soils and climax plant communities can both be thought of as products of the same set of environmental variables—climate, organisms, relief, parent material, and time—and an interdependence therefore exists between a specific soil body and its climax vegetation (Hironaka *et al.* 1991). Considerable research in forests and rangelands of the western U.S. has been directed at identifying and even attempting to quantify the relationships between soils and the native climax communities they support (Daubenmire 1970; Steele *et al.* 1981; Hironaka *et al.* 1983; Tisdale and Bramble-Brodahl 1983; Cooper *et al.* 1991).

The habitat type (h.t.) approach to classification of land areas was first introduced by Daubenmire (1952) and is based on identification of potential climax plant communities. This system has been widely used to stratify and classify forest lands in the western U.S. (Pfister *et al.* 1977; Steele *et al.* 1981; Cooper *et al.* 1991). Habitat types represent a “type” rather than “continuum” approach to classification—they are identified by a specified combination of indicator plant species that reflect a modal type. Soil classification also represents a “type” approach. Soil taxa are defined in Soil Taxonomy by a discrete set of diagnostic chemical, physical, and morphological properties, many of which influence or are a product of the native vegetation (Soil Survey Staff 1975).

Given these similarities between soil and habitat type classification schemes, soil classification should be related to a habitat type classification within a given environmental setting. However, efforts to correlate soil and habitat type classifications have not been entirely successful. Potkin (1991) found that many soil properties which are important to plant community distributions in

high-elevation environments are not utilized by Soil Taxonomy for classification purposes. Neiman (1986) examined 89 forested sites throughout northern Idaho and found little quantitative relationship between h.t.'s and soil physical properties and taxonomic classes. These studies suggest that within some environmental settings, soil classification does not emphasize or consider characteristics that are important to the distribution of plant communities. Furthermore, Hironaka *et al.* (1991) have cautioned that at any scale beyond a very localized application, a universal correlation does not exist between soil properties and vegetation attributes.

In northern Idaho, volcanic ash has had a significant impact on many soil properties and is believed to strongly influence the distribution of vegetation (Steele *et al.* 1981). Recent changes in Soil Taxonomy (Soil Survey Staff 1975) have placed more importance on the unique properties of ash-influenced soils. Once ash has been deposited across a region, it is exposed to various soil weathering environments and surficial processes such as erosion. As a result, the impact of the ash on soil properties may be quite variable within a relatively small geographic region. Accordingly, the Andisol order has been added along with Andic and Vitrandic intergrades of other orders to better reflect a range in ash-influenced soil properties (Soil Survey Staff 1992).

Given the importance of volcanic ash as a soil parent material in many forested areas of the Pacific Northwest and the increased taxonomic sensitivity to ash-influenced soils, the objective of this study is to illustrate some of the interrelationships that exist between soils and plant communities in this region. Specifically, this paper compares the properties and classification of soils and vegetation along a south-facing elevational gradient in the Selkirk Mountains of northern Idaho.

Methods And Materials

Study Area

The study area is located in the Trout Creek drainage of the Selkirk Mountains in northern Idaho (Figure 1). Trout Creek flows from Pyramid Lake to the Kootenai River, dropping approximately 1300 m in elevation over a distance of 20 km. The general topography of the drainage becomes steeper at lower elevations as Trout Creek has incised more deeply into the underlying substrate. Two contrasting geologic substrates occur in this

area of the Selkirks. Steeply dipping Precambrian metasediments flank the range on the east side and granitic rocks of the Kaniksu Batholith make up the core of the range (Conners 1976). Pleistocene glacial deposits overlie both substrates and thus constitute one of the major soil parent materials of the area. During the Holocene, large quantities of volcanic ash from the cataclysmic eruption of Mount Mazama (approximately 6700-6800 yrs BP) were deposited throughout the region (Fryxell 1965; Fosberg *et al.* 1979; Bacon 1983). Some of this ash has been retained in modern soils either as a relatively undisturbed surficial mantle or as an admixture with coarser-textured granitic materials. The 1800 AD eruption of Mount St. Helens added an additional 1-3 cm of ash (Layer T) to many soils of the area (Smith *et al.* 1968; Okazaki *et al.* 1972; Smith *et al.* 1975; Mullineaux 1986). This thin ash layer has been preserved in many of the soils, indicating relatively little surface disturbance has taken place over the past 200 yrs. Ash from the 1980 Mount St. Helens eruption was not observed in this area.

The climatic regime of the Trout Creek area is an inland expression of the Pacific Coast maritime climate. The closest weather station is located approximately 11 km south of the study area at 1677 m elevation. Data from this station indicate annual precipitation averages 1180 mm and mean annual air temperature is 2.6°C (Cooper *et al.* 1991). Along the Trout Creek elevational gradient, precipitation is estimated to range from 560 to 2000 mm and falls primarily in the spring, fall, and winter (Houston 1988). Summers are generally warm and dry.

Study sites within the Trout Creek drainage were selected to represent the variation in soils and habitat types observed along elevational gradients in this part of the Selkirk Mountains. Sites chosen for sampling were restricted to those having mature vegetation stands that were relatively undisturbed by logging or fire. Of the 30 sites sampled and described by Houston (1988), we will report data from four sites which collectively encompass the range in observed soil characteristics and potential climax plant communities (Figure 1). All four sites are located on south-facing, relatively stable ridge slopes.

Soils

Within each of the climax plant communities, soils were examined using road cuts and shallow

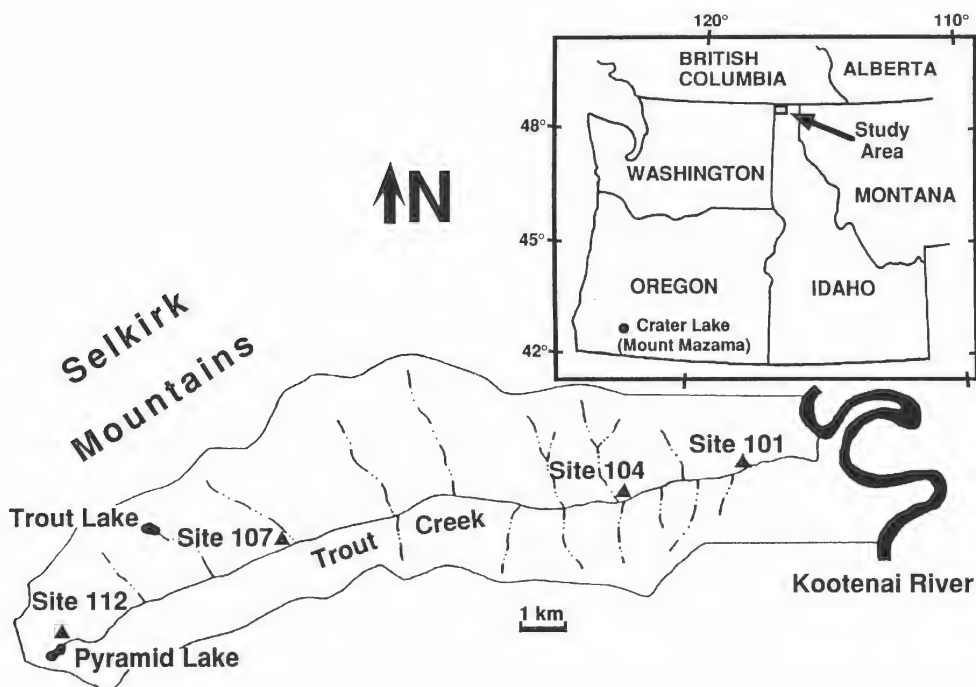


Figure 1. Map showing location of study area (inset) and sampling sites within the Trout Creek drainage.

hand-dug pits to determine representative morphological characteristics. A sampling pit was then located near the center of the plant community and dug to a depth of approximately 1 m. Soil profiles were described using standard horizon designations and descriptions (Soil Conservation Service 1984; Soil Survey Staff 1992). Soils were sampled by genetic horizons and classified to the family level according to Soil Taxonomy (Soil Survey Staff 1992) using appropriate laboratory and soil climate data. Samples were air dried and crushed with a rubber-tipped pestle to pass a 2-mm sieve. Laboratory analyses were performed using the following methods: particle-size analysis by pipette and centrifugation procedures (Jackson 1975; Gee and Bauder 1986); water retention at 1.5 MPa of soil moisture tension using pressure-plate extraction (Klute 1986); organic carbon by rapid dichromate oxidation (Nelson and Sommers 1982); pH (1:1 soil:water) and NaF pH using a combination glass electrode (Soil Conservation Service 1984); P retention by colorimetry (Blakemore *et al.* 1981); and Fe and Al contained in short-range order minerals by extraction with acid ammonium oxalate (Soil Conservation Service 1972). Glass con-

tents were determined on very fine sand fractions by counting between 100 and 200 grains using a petrographic microscope.

Vegetation

A 375m² circular vegetation plot was established at each soil sampling location. All vascular plant species present within this area were identified according to Hitchcock and Cronquist (1973) and their abundance recorded by canopy coverage class (Cooper *et al.* 1991) (Table 1). Habitat types and phases were identified using a forest habitat type guide for northern Idaho (Cooper *et al.* 1991).

Results and Discussion

The distribution of soil and forest climax community classifications along the Trout Creek climatic gradient are summarized in Figure 2. The approximate ranges of soil moisture and temperature regimes are also given. These regimes are based on data collected at the sites (Fosberg, unpublished data) and related studies in northern Idaho by Schauer (1976). Cryic and frigid soil temperature

TABLE 1. Species list and coverage classes¹ for Trout Creek sites.

	Site 112	Site 107	Site 104	Site 101
Trees				
<i>Pinus ponderosa</i>	0	0	0	2
<i>Pseudotsuga menziesii</i>	0	T	T	3
<i>Larix occidentalis</i>	0	T	0	0
<i>Pinus monticola</i>	0	T	0	0
<i>Thuja plicata</i>	0	3	4	0
<i>Tsuga heterophylla</i>	0	1	3	0
<i>Picea engelmannii</i>	2	1	0	0
<i>Abies lasiocarpa</i>	3	2	0	0
<i>Pinus albicaulis</i>	3	0	0	0
Shrubs				
<i>Holodiscus discolor</i>	0	0	0	3
<i>Physocarpus malvaceus</i>	0	0	0	4
<i>Philadelphus lewisii</i>	0	0	0	2
<i>Spirea betulifolia</i>	0	0	0	T
<i>Symphoricarpus albus</i>	0	0	0	2
<i>Berberis repens</i>	0	0	T	3
<i>Amelanchier alnifolia</i>	0	0	T	1
<i>Rosa gymnocarpa</i>	0	0	0	1
<i>Acer glabrum</i>	0	0	1	0
<i>Vaccinium myrtillus</i>	0	0	T	0
<i>Pachistima myrsinites</i>	0	1	1	T
<i>Lonicera utahensis</i>	0	1	T	0
<i>Linnaea borealis</i>	0	1	T	0
<i>Vaccinium globulare</i>	3	2	0	0
<i>Sorbus scopulina</i>	T	0	0	0
<i>Rhododendron albiflorum</i>	5	0	0	0
Forbs				
<i>Aralia nudicaulis</i>	0	0	T	T
<i>Disporum hookeri</i>	0	T	T	T
<i>Smilacina stellata</i>	0	T	T	0
<i>Achillea millefolium</i>	0	0	0	T
<i>Smilacina racemosa</i>	0	0	T	T
<i>Hieracium albiflorum</i>	0	0	0	T
<i>Goodyera oblongifolia</i>	0	T	T	0
<i>Chimaphila umbellata</i>	0	0	T	0
<i>Trillium ovatum</i>	0	0	T	0
<i>Pyrola secunda</i>	0	T	T	0
<i>Clintonia uniflora</i>	0	T	T	0
<i>Chimaphila menziesii</i>	0	T	0	0
<i>Tiarella trifoliata</i>	0	T	0	0
<i>Osmorhiza chilensis</i>	0	0	T	0
<i>Viola orbiculata</i>	0	T	T	0
<i>Mitella breweri</i>	T	0	0	0
<i>Xerophyllum tenax</i>	1	0	0	0
Graminoids				
<i>Agropyron spicatum</i>	0	0	0	1
<i>Calamagrostis rubescens</i>	0	0	0	2
<i>Carex geyeri</i>	0	0	0	T
<i>Bromus vulgaris</i>	0	T	0	T
<i>Luzula hitchcockii</i>	3	0	0	0

¹ 0 = not present; T = 0-1% canopy coverage; 1 = 1-5%; 2 = 5-25%; 3 = 25-50%; 4 = 50-75%; 5 = 75-95%; 6 = 95-100%.

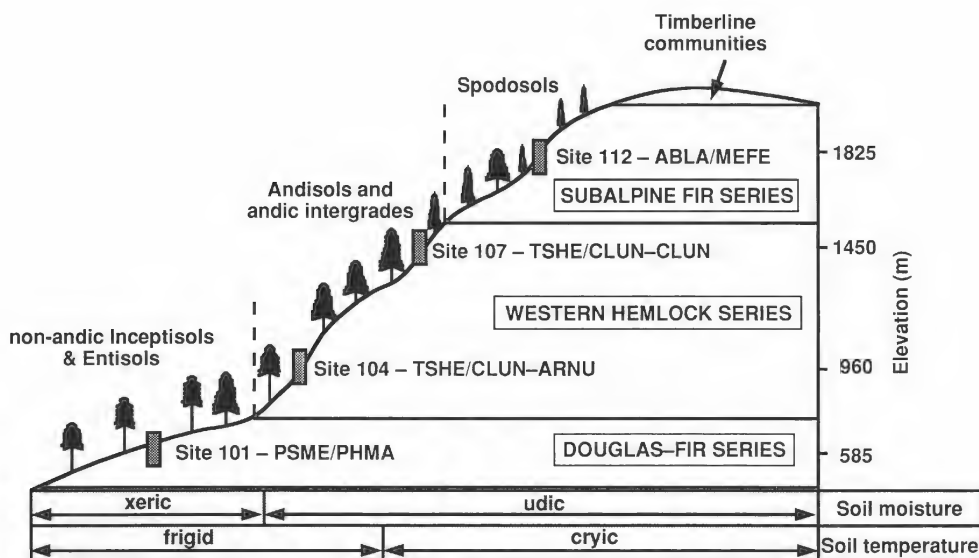


Figure 2. Generalized soil-plant community relationships on a south-facing slope in the Trout Creek drainage. Abbreviations: ABLA/MEFE = *Abies lasiocarpa*/*Menziesia ferruginea* h.t.; TSHE/CLUN-CLUN = *Tsuga heterophylla*/*Clintonia uniflora* h.t., *Clintonia uniflora* phase; TSHE/CLUN-ARNU = *Tsuga heterophylla*/*Clintonia uniflora* h.t., *Aralia nudicaulis* phase; PSME/PHMA = *Pseudotsuga menziesii*/*Physocarpus malvaceus* h.t.

regimes are both characterized by a mean annual soil temperature $< 8^{\circ}\text{C}$, but the cryic regime has cooler summer temperatures (Soil Survey Staff 1992). Udic and xeric soil moisture regimes differ in the length of time that the soil is dry during the summer months—xeric soils are subject to longer periods of dry conditions than are udic soils (Soil Survey Staff 1992). In the Trout Creek drainage, the change from cryic to frigid temperature regimes occurs somewhere within the *Tsuga heterophylla* zone. The change from the udic to xeric moisture regime appears to coincide with the change from the *T. heterophylla* series to the *Pseudotsuga menziesii* series.

The highest elevation sampling location, Site 112, is located at an elevation of 1830 m on a 10% slope and represents the coldest and moistest end of the climatic gradient. Climax vegetation is classified as an *Abies lasiocarpa*-*Menziesia ferruginea* (fool's huckleberry) h.t., *Luzula hitchcockii* (smooth woodrush) phase. The soil has formed in a mantle of Mazama ash overlying coarse-textured glacial drift (Figure 3). The dominant feature of this soil is the morphological evidence of podzolization. In the podzolization process Fe and Al move as solu-

ble metal-organic and inorganic complexes, giving rise to a light-colored E horizon which overlies a brown to reddish-brown Bs (or Bhs) horizon. Sufficient quantities of Fe and Al have been translocated at Site 112 to form an albic (E)—spodic (Bs) horizon sequence (Figure 3; Table 2). Accordingly, this soil is now classified as a Spodosol, which is defined in Soil Taxonomy as a soil in which substantial quantities of amorphous Al and Fe (oxalate-extractable) have accumulated beneath an albic E horizon (Soil Survey Staff 1992). Previously this soil had been classified as an Andisol (Soil Survey Staff 1990) and an Andept (Soil Survey Staff 1975).

In the Trout Creek drainage, we have observed the E-Bs horizon sequence (and Spodosols) only in association with the subalpine fir series. Similar associations have been reported elsewhere in the Pacific Northwest (Smith *et al.* 1968; Hunter 1988; Dahlgren and Ugolini 1991). This soil-plant community association exists because the conditions required for subalpine fir climax are also conducive for podzolization. The vegetation and climate interact in a manner to provide soluble organic chelating compounds and relatively large quantities of soil moisture that cause downward

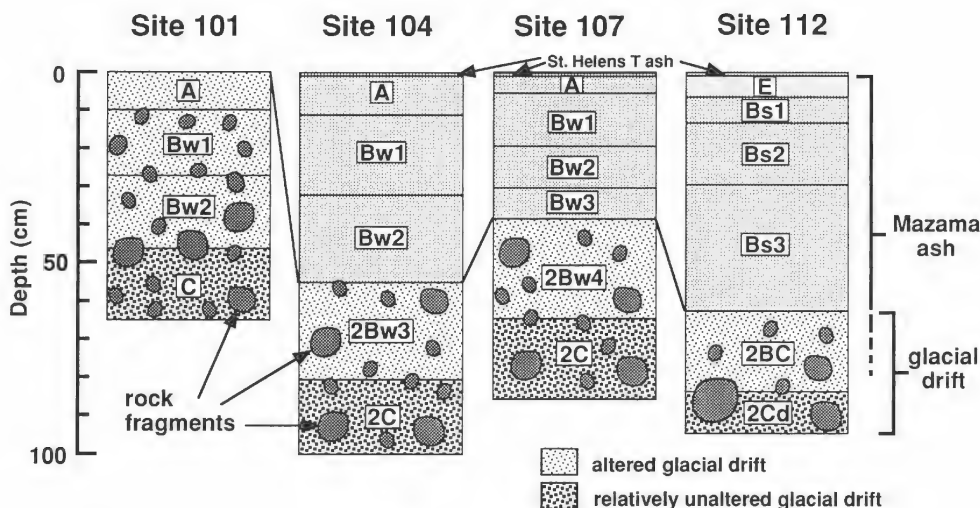


Figure 3. Comparison of parent material and horizon sequences in Trout Creek soils sampled along a bioclimatic gradient.

migration of organic and inorganic metal complexes.

The Site 112 soil is the most strongly acid and contains the largest quantities of organic matter of any of the soils in this study (Table 2). NaF pH values > 10 , high P retention, and comparatively high glass contents in the very fine sand fractions all indicate a strong volcanic ash influence and result in classification of this Haplocriod as an Andic intergrade. Relatively large quantities of oxalate-extractable Fe and Al in the Bs horizons reflect the greater intensity of weathering and podzolization processes in this soil compared to those of the other sites.

Site 107 is located on a 35% slope at an elevation of 1450 m. Vegetation fits the *T. heterophylla*-*Clintonia uniflora* (queencup beadlily) h.t., *Clintonia uniflora* phase. The presence of *Abies lasiocarpa* and *Picea engelmannii* (Engelmann spruce) at this site suggest it occupies the cooler, moister end of the *T. heterophylla* series. The soil has formed in similar parent materials to those at Site 112, as high NaF pH values, high P retention, and comparatively high glass content all indicate a strong volcanic ash influence (Figure 3, Table 2). The major morphological difference is that podzolization processes have not been sufficient to produce an E-Bs horizon sequence. The Bw horizons do, however, exhibit sufficient development to meet the requirements of a cambic

diagnostic horizon. The strong influence of volcanic ash and the lack of a spodic horizon result in classification of this soil as an Andisol (Soil Survey Staff 1992). This soil had previously been classified as an Andept (Soil Survey Staff 1975) and was therefore not distinguished from the Site 112 soil at the higher levels of Soil Taxonomy despite major differences in soil-forming processes.

Site 104 is located on a 55% slope at an elevation of 960 m and represents the lower-elevation end of the *T. heterophylla* series. Vegetation is classified as a *T. heterophylla*-*C. uniflora* h.t., *Aralia nudicaulis* (wild sarsaparilla) phase. Cooper *et al.* (1991) described this as the warmest and generally moistest phase of this habitat type, but also observed relatively dry stands that are barely able to support the moist-site species. Even though this site has the same h.t. classification as Site 107, the absence of *A. lasiocarpa* and *Picea engelmannii* indicates comparatively warmer and drier conditions. The sandy textures and relatively low water content at 1.5 MPa of soil moisture tension further suggest that this is a droughty site (Table 2). We feel the *A. nudicaulis* phase at Site 104 represents a warmer, drier environment than does the *C. uniflora* phase at Site 107. Cooper *et al.* (1991), however, describe the *C. uniflora* phase as the driest and warmest phase of the *T. heterophylla*-*C. uniflora* h.t.

TABLE 2. Selected morphological, chemical, and physical properties of Trout Creek soils described in this study.

Horizon	Depth (cm)	Color		Sand	Silt	Clay	pH		Organic carbon	1.5 MPa H ₂ O	P retention	Oxalate- extractable		Glass vfs*
		moist	dry				H ₂ O	NaF				Fe	Al	
----- % -----														
Site 112	medial over loamy-skeletal		Andic Haplocryod											
Oi, Oe	5-0													
C	0-1	2.5Y 5/2	10YR 7/2	(St. Helens T ash)										
E	1-6	10YR 4/2	10YR 6/1	38.3	56.2	5.5	3.7	7.3	4.8	14.6	20.1	<0.1	0.1	38
Bs1	6-13	7.5YR 4/5	10YR 5/5	39.3	54.5	6.2	4.7	10.8	4.2	18.5	96.4	1.3	2.1	24
Bs2	13-29	7.5YR 4/5	10YR 6/5	39.1	55.6	5.4	5.4	10.9	2.7	13.2	95.9	0.7	1.8	28
Bs3	29-62	10YR 4/5	10YR 6/5	45.0	51.0	4.0	5.2	10.8	1.4	8.7	86.6	0.5	1.2	22
2BC	62-83	2.5Y 4/4	2.5Y 7/4	51.7	45.1	3.2	5.3	10.6	0.7	6.2	55.3	0.2	0.6	2
2Cd	83-95+	2.5Y 4/2	2.5Y 5/2	68.0	29.3	2.7	4.9	10.3	0.6	5.1	30.5	0.1	0.3	1
Site 107	ashy over sandy-skeletal, mixed		Typic Vitricryand											
Oi, Oe	5-0													
C	0-1	2.5Y 5/2	10YR 7/2	(St. Helens T ash)										
A	1-5	7.5YR 3/4	10YR 4/4	64.8	31.0	4.1	5.0	10.4	2.9	6.5	54.2	0.5	1.2	31
Bw1	5-18	7.5YR 3/4	10YR 4/4	62.0	34.6	3.5	5.2	10.6	2.8	7.2	70.9	0.6	1.5	32
Bw2	18-30	10YR 3/5	10YR 5/5	65.6	31.2	3.2	5.2	10.5	1.8	4.4	64.1	0.4	1.4	32
Bw3	30-38	10YR 3/5	10YR 5/5	69.9	27.8	2.3	5.2	10.5	1.3	4.6	62.8	0.4	1.4	37
2Bw4	38-64	10YR 4/5	10YR 6/5	83.4	14.9	1.8	5.2	10.0	0.4	1.8	23.8	0.2	0.4	4
2C	64-85+	2.5Y 5/4	2.5Y 6/4	93.6	5.6	8.9	5.1	9.5	0.1	0.9	17.7	0.1	0.1	0
Site 104	sandy-skeletal, mixed, frigid		Vitrandic Udorthent											
Oi, Oe	8-0													
C	0-1	2.5Y 5/2	10YR 7/2	(St. Helens T ash)										
A	1-11	7.5YR 3/4	10YR 5/4	80.5	16.3	3.2	5.6	9.8	1.0	4.4	26.4	0.3	0.4	7
Bw1	11-32	7.5YR 4/4	10YR 5/4	82.0	15.5	2.6	6.0	9.7	0.6	3.7	23.9	0.3	0.4	5
Bw2	32-55	7.5YR 4/5	10YR 5/5	84.9	13.6	1.5	6.1	9.9	0.4	3.4	24.4	0.3	0.3	2
2Bw3	55-80	2.5Y 4/5	2.5Y 6/5	90.9	8.1	1.0	6.1	9.4	0.2	2.2	19.1	0.2	0.2	1
2C	80-100+	2.5Y 4/4	2.5Y 6/4	92.5	6.9	0.7	5.9	8.8	0.1	1.4	16.2	0.2	0.1	0
Site 101	loamy-skeletal, mixed, frigid		Typic Xerochrept											
Oi, Oe	4-0													
A	0-10	10YR 3/2	10YR 4/3	64.9	28.3	6.8	6.1	8.4	1.2	4.0	27.0	0.5	0.2	2
Bw1	10-27	10YR 3/4	10YR 5/4	68.4	25.4	6.2	6.2	8.4	0.7	3.0	25.8	0.5	0.1	0
Bw2	27-46	10YR 3/4	10YR 5/4	61.5	32.7	5.8	5.9	8.7	0.8	3.0	26.5	0.5	0.2	0
C	46-64+	10YR 4/3	10YR 6/3	77.5	19.7	2.8	5.7	7.8	0.2	1.4	25.1	0.3	>0.1	0

*very fine sand

Steep slopes and greater susceptibility to fire and subsequent erosion associated with this drier site may have resulted in removal of much of the volcanic ash. There is only moderate ash influence on this coarse-textured soil as evidenced by intermediate NaF pH values, low P retention, and small quantities of glass in the very fine sand fraction, resulting in classification as a Vitrandic Udorthent. This classification indicates the soil has some of the characteristics associated with volcanic ash-derived soils, but they are too weakly expressed for inclusion in the Andisol order (Soil Survey Staff 1992). Development of Bw horizons results in classification as either an Entisol or Inceptisol, depend-

ing on soil texture (Soil Survey Staff 1992) and both of these soil orders are well-represented throughout this vegetation zone.

Site 101 is located on a 50% slope at an elevation of 585 m and represents the warmer, drier end of the climatic gradient observed in the Trout Creek drainage. Parent material is glacial drift and vegetation is classified as a *P. menziesii*-*Physocarpus malvaceus* (ninebark) h.t., *Physocarpus malvaceus* phase. *Pinus ponderosa* (ponderosa pine), absent from the higher-elevation sites, and Douglas-fir are the only tree species. The increased abundance of graminoids has resulted in formation of the darkest A horizon of any of the soils

examined in this study. There is also sufficient B horizon development to meet the requirements for a cambic horizon, resulting in placement of the soil into the Inceptisol order. There is little or no volcanic ash influence and the soil is therefore classified as a Typic (rather than Andic or Vitrandic) Xerochrept (Soil Survey Staff 1992). Throughout this region, it has been observed that Mazama ash is usually absent in soils associated with Douglas-fir h.t.'s (Barker 1981; Weisel 1982). During the warmer, drier conditions that existed at the time of the cataclysmic eruption of Mt. Mazama, these sites most likely did not have sufficient canopy cover to prevent erosion of the ash that presumably was deposited uniformly throughout the area.

Conclusions

In the Trout Creek drainage of northern Idaho, Spodosols formed in volcanic ash are associated with the *A. lasiocarpa* series at the higher elevations. Classification of these soils is determined by the albic-spodic horizon sequence. These soils are also classified as intergrades to the Andisol order because of the strong volcanic ash influence. Habitat types of the *T. heterophylla* series occupy the middle elevations. Andisols are the dominant soils at the moister and cooler end of this zone. At the warmer, drier end of the western hemlock zone, there has been less influence of volcanic ash on soil properties. Accordingly, soils are classified as

Andic (and Vitrandic) intergrades of Inceptisols and Entisols. The *P. menziesii* series occupies the frigid and xeric climatic regime of the lower elevations. Soils have little or no volcanic ash influence and, based on our data, are placed in Typic rather than Andic or Vitrandic subgroups of Inceptisols and Entisols.

This study illustrates some of the changes in soil properties that occur in association with different habitat types along elevational gradients in the Selkirk Mountains. These changes reflect differences in volcanic ash influence, climate, and various soil-vegetation interactions. Because recent changes in Soil Taxonomy better recognize the range of characteristics in soils such as these, we suggest that many quantifiable relationships exist between vegetation and soil classification systems in volcanic ash-influenced regions of the Pacific Northwest. We further suggest these relationships can be utilized by resource managers and field scientists as a means of extrapolating limited amounts of data that exist for these forested ecosystems.

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Rosemary H. Leach,¹ Montana Cooperative Wildlife Research Unit,² University of Montana, Missoula, Montana 59812 and

W. Daniel Edge, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331

Summer Home Range and Habitat Selection by White-tailed Deer in the Swan Valley, Montana

Abstract

We studied summer habitat use by 13 adult and 5 yearling female white-tailed deer (*Odocoileus virginianus*) in the Swan Valley, Montana during 1980 and 1981. We used 515 radio relocations to evaluate use of habitats within home ranges and selection of home ranges within the study area. All deer used riparian habitats more, and upland habitats less than expected based on availability within their summer home ranges. Adult deer home ranges contained more logged riparian and unlogged upland habitat than randomly-placed polygons, called random home ranges. Adult home ranges also contained less logged upland habitat than random home ranges. Yearling home ranges generally resembled random home ranges in habitat composition; however, random home ranges contained less logged riparian habitat than did yearling home ranges. Based on selection for unlogged riparian habitat within home ranges and an inverse relationship between adult home range size and the availability of unlogged riparian habitat within their home range, it appeared that unlogged riparian habitat was seasonally important to deer in the Swan Valley. Based on our results, we recommend that riparian habitats, particularly unlogged ones, be managed conservatively by establishing buffer zones of no logging. Harvest should be limited to uneven-aged silvicultural systems. Quality upland cover should be maintained adjacent to riparian areas and other moist habitat components. Habitat diversity on a small scale should be a management goal and could be accomplished with uneven-aged silviculture and prescribed fire. Alternatively, when even-aged management is applied, cutting unit size should be minimized (≤ 12 ha) and units dispersed over the landscape. Postlogging scarification should be limited to the minimum required for successful conifer regeneration in order to enhance shrub production for deer forage and cover.

Introduction

White-tailed deer are an important big game species in northwestern Montana, where its distribution is strongly correlated with the distribution of coniferous forest habitat (Mundinger 1984). Summer habitat use by white-tailed deer has been described in various parts of North America (Allen 1968, Martinka 1968, Drolet 1976, Tierson *et al.* 1985). Although several previous studies focused on the winter ecology of white-tailed deer in the Swan Valley (Weckwerth 1958, Hildebrand 1971, Mundinger 1984), similar studies of summering deer in northwestern Montana have not been conducted. Increased timber harvest in northwestern Montana has also raised concerns about the impacts of forest practices to local white-tailed deer (Mundinger 1984).

Johnson (1980) recognized that selection occurs on several scales. Inferences from habitat selection analyses on 1 scale will likely differ from inferences made on another scale, and consequently, ecological interpretations and management

recommendations may be scale-dependent. Our objective was to identify preferred summer habitat of white-tailed deer in the managed forests of the Swan and Clearwater Valleys of Montana at 2 scales: the distribution of home ranges within the study area (2nd-order selection), and the selection of habitat categories within the home range (3rd-order selection).

Study Area and Methods

The Swan-Clearwater summer range includes the southern half of the Swan Valley and the northern quarter of the adjacent Clearwater Valley. This area was described previously by Antos (1977) and Mundinger (1981). The study area was approximately 675 km² with elevations ranging from 1,060 m on the valley floor to 1,575 m on the mid-slopes of the mountains. Unique vegetative characteristics and habitat mosaics found within the study area result from the maritime climate and diverse soil moisture regimes. The major habitat types found on the study area were within the moist subalpine fir (*Abies lasiocarpa*), western red cedar (*Thuja plicata*), spruce (*Picea* spp.), and grand fir (*Abies grandis*) series (Pfister *et al.* 1977). However, most sites were dominated by seral species including lodgepole pine (*Pinus contorta*), Douglas-

¹Current address: Wildlife Resource Management Program, Yakima Indian Nation, P.O. Box 151, Toppenish, WA 98948

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fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), and ponderosa pine (*Pinus ponderosa*). Timber harvest (clearcut or selection cut) was the dominant land use within the study area with clearcuts ranging from 2-260 ha in size and 1-25 years in age, located throughout the study area (Mundinger 1984). Approximately half of the study area had been logged.

Our analysis focused on deer use of 4 major habitat categories: unlogged and logged uplands, and unlogged and logged riparian areas. We classified an area as riparian if water (surface or subsurface) influenced vegetation such that wet-site indicator plants were present (Pfister *et al.* 1977). Overstory species composition was similar between riparian and upland sites; however, trees associated with moist habitat types occurred with higher frequency in riparian habitats. We defined clearcuts, partial cuts, and second growth stands as logged habitat. There were no discernible differences in overstory species logged or harvest practices between riparian and upland habitats. Understory species were similar between logged and unlogged sites and between riparian and upland sites in general; however, moist-site indicator species were more common in riparian habitats.

Deer were captured in clover traps (Clover 1956) on winter range of the upper Swan Valley (Mundinger 1984). Thirteen adult and 5 fawn females were radiocollared and released. Radioed deer were relocated on summer ranges during 1980 and 1981 by aerial (25%) and ground (75%) tracking between 0800 and 1700 h. Aerial telemetry was done from a Cessna 182 according to the methodology of Gilmore *et al.* (1981), and relocation error was estimated to be approximately 100-150 m. Ground tracking included triangulated fixes (14%) and close-range tracking (86%) using a hand-held yagi antenna. Triangulations generally were based on 3 compass bearings and were used only when evidence indicated that the animal was within 100-600 m, when triangulation polygons were relatively small and contained only 1 discrete habitat category, and when no topographic barriers existed between the observer and the estimated position of the deer. Deer locations based on triangulations were in close proximity to those determined from close-range tracking. Close-range tracking was conducted until the animal was seen or disturbed enough to move.

All deer locations were plotted on 1:15,840 topographic maps and aerial photos. Summer home ranges were estimated using the minimum convex

polygon (MCP) method (Mohr 1947). Five adults and 5 yearlings were tracked for 1 summer, and 8 adults were followed for 2 summers. Summer home range estimates for the 8 deer tracked 2 summers were calculated for each summer separately in order to make these estimates comparable to those for deer tracked only 1 summer. The number of radiolocations obtained each summer for each deer averaged 19.8 (range = 9-36).

The interval between relocations ranged from 2 hours to 1 week; most relocations of the same individual were separated by ≥ 24 hours. One deer that was followed for 1 summer used inaccessible wilderness and could be relocated only after a lengthy hike. This deer was relocated repeatedly at relatively short intervals during wilderness stays that ranged from several hours to 2 days. These relocations would potentially be more prone to autocorrelation bias (Swihart and Slade 1985), and the size of her summer home range may have been underestimated; however, this female's habitat use data were similar to those of other adults based on tests of habitat selection by individual deer (Leach 1982) and were included in a pooled habitat use analysis on this basis. Three deer were relocated hourly for 24 hours to determine if they ventured beyond the home ranges delineated by relocations obtained at the more widely spaced intervals described above. All of the relocations from these tracking sessions fell within the home ranges delineated by the longer interval relocations.

We assessed the selection of home ranges within the study area (2nd-order selection; Johnson 1980) by comparing deer home ranges to 15 randomly selected areas called random home ranges. Random home ranges were of similar size, shape, and elevation as deer home ranges delineated during 1980. We constructed a grid of the study area and randomly selected coordinates that served as the center for each random home range. The availability of the 4 habitat categories was estimated on deer home ranges using a dot grid for discrete data (Marcum and Loftsgaarden 1980). The expected availabilities of the 4 categories in random home ranges was measured with a digital planimeter. The analysis then proceeded according to the methodology of Neu *et al.* (1974).

A habitat diversity index was calculated for each deer and random home range by summing the number of discrete habitat types (≥ 0.5 ha) and riparian habitat polygons (e.g., seeps, ponds, potholes, creeks) and dividing by the overall deer or random home range. These indices were then

standardized on a 100-ha basis. An average standardized diversity index for deer and random home ranges was then calculated.

Third-order deer habitat selection (Johnson 1980) was analyzed by comparing use of the 4 habitat categories by all deer with the availability of the same categories from deer home ranges (8 adult ranges estimated from 2 summers of tracking and 5 adult and 5 yearling ranges from 1 summer of tracking) (Neu *et al.* 1974). The 4 habitat categories were mapped within home ranges, and availability was determined using a digital planimeter. Simultaneous 90% confidence intervals were determined for the pooled use (radiolocations) of the 4 categories. If the calculated confidence interval for deer use of a given component did not contain the true availability of that component, use was considered statistically significant, indicating either preference or avoidance of that component.

We used Mann-Whitney tests (Daniel 1978:82-86) to test for differences in home range size between yearling and adult deer, and for differences in diversity indices between deer and random home ranges. We related deer home range size to the proportion of each of the 4 habitat categories available using the Spearman rank coefficient (r_s). We used nonparametric tests because data were not normally distributed.

Results

Home Range

We collected 515 radio relocations from May-September, 1980 and 1981. Deer summer home ranges were 6-40 km south of their winter home ranges. Unlike their winter distribution, deer summer home ranges were widely dispersed and adult ranges did not overlap. Four adult-yearling pairs had overlapping home ranges. Two of these pairs were clearly mother and daughter; the familial relationships of the other 2 were unknown.

Marked animals used the same area each summer. Home ranges of each of the 8 adults monitored for 2 summers overlapped an average of 44% between years, and their activity centers were the same (Gladfelter 1978). These animals also had used these same summering areas during 1979 (Mundinger, Mont. Dept. Fish, Wildlife, and Parks, unpubl. data).

Single-summer home ranges for adult deer averaged 70 ha (SE = 25.9) during 1980 ($n = 10$) and 71 ha (SE = 18.4) during 1981 ($n =$

11). The ranges of 5 yearlings averaged 91 ha (SE = 30.4) and did not significantly differ from those of 11 adults followed that year (Mann-Whitney test, $P = 0.25$). Plots of home range size versus increasing numbers of relocations showed 17 of 26 single-summer home ranges had reached an asymptote, suggesting they were based on an adequate number of relocations (Odum and Kuenzler 1955). The remaining 9 single-summer home ranges may have been underestimated slightly. The average MCP estimate for these 9 home ranges was, however, similar to the average for the 17 adequately sampled home ranges.

2nd-Order Selection

The summer home ranges of adult deer differed from random home ranges relative to 3 habitat categories ($P < 0.10$). Adults selected home ranges with more logged riparian, more unlogged upland and less logged upland than was available on the study area (Figure 1). In contrast, summer home ranges of yearling deer were similar to random home ranges except that yearling ranges contained more logged riparian habitat ($P < 0.10$, Figure 1). The proportion of unlogged riparian habitat within a deer home range was inversely correlated with home range size for adults ($r_s = -0.43$, $P < 0.05$), but was not correlated with home range size for yearlings ($r_s = 0.425$, $P > 0.10$). In contrast, the proportion of logged riparian habitat within summer home ranges was positively correlated with

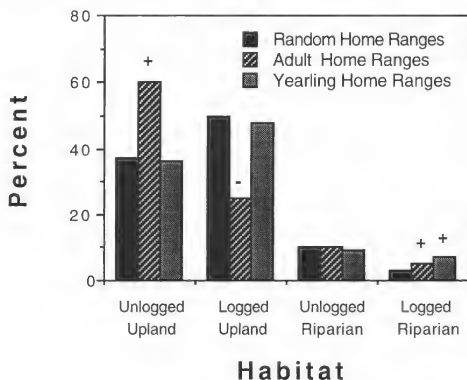


Figure 1. Percent habitat composition of 13 adult and 5 yearling white-tailed deer home ranges compared to 15 random home ranges in the Swan-Clearwater River Valleys, Montana, during 1980 and 1981. + or - indicates that deer home range habitat composition differs ($P \leq 0.1$) from random home ranges.

home range size for adult deer ($r_s = 0.48$, $P < 0.05$), but not for yearlings ($r_s = -0.63$, $P > 0.10$). We found no correlation between home range size and the proportion of upland habitats within a home range for either age class. Summer home ranges of deer contained an average of 2 cutting units that averaged 12 ha/100 ha of home range for adults and 25 ha/100 ha of home range for yearlings.

Twenty-four different habitat types were found in deer summer home ranges. Habitat types representing cool, moist environments were most common. Sixteen were within the spruce, grand fir, western red cedar series, and mesic types within the subalpine fir series. Home ranges of adults contained an average of 9 habitat types/100 ha; yearling ranges ($n = 4$) averaged 10 habitat types/100 ha. Twenty-two habitat types were found in random home ranges, 20 of which also were found in deer home ranges. The most common habitat types in deer home ranges were generally uncommon in random home ranges; common types in random home ranges were also uncommon in deer home ranges. Average diversity indices, 13.4 for adults and 14.8 for yearlings, were significantly higher than average indices for random home ranges (7.7) (Mann-Whitney test, $P = 0.004$).

3rd-Order Selection

Collectively, use of habitat categories within home ranges by adults and yearlings was similar, but differed from availability for all 4 habitat categories ($P < 0.10$) (Figure 2). Both adults and yearlings were relocated more frequently in riparian habitats (logged and unlogged) and less frequently in upland habitats than expected, based on habitat availability. No individual deer used a riparian component less than expected. Two deer (1 adult and 1 yearling) used logged riparian habitat more than expected. Unlogged riparian habitat was scarce on their ranges, and the logged riparian habitat had residual conifers and a dense cover of paper birch (*Betula papyrifera*), alder (*Alnus sinuata*), red-osier dogwood (*Cornus stolonifera*), and willows (*Salix* spp.). No deer used upland habitats more than expected.

Discussion

White-tailed deer in the Swan-Clearwater region used the same summer home ranges each year. In addition, natal home ranges of female fawns defined their home range areas as adults. Both of

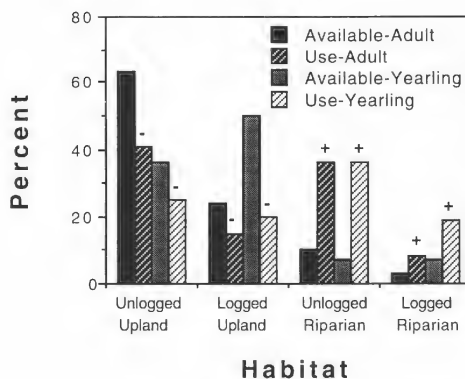


Figure 2. Percent use and availability of habitat categories within 13 adult and 5 yearling deer home ranges in the Swan-Clearwater River Valleys, Montana, during 1980 and 1981. + or - indicates that use differs ($P \leq 0.1$) from availability.

these patterns have been documented elsewhere (Verme 1973, Hoskinson and Mech 1976, Janke 1977, Nelson 1979, Nelson and Mech 1981, Tier-son *et al.* 1985), and may contribute to enhanced survival and reproductive success.

Average home range size in this study was smaller than that reported in other studies (Sparrowe and Springer 1970, Hoskinson and Mech 1976, Janke 1977, Nelson and Mech 1981, Tier-son *et al.* 1985). Small home range size may have been related to the quality of habitats on the Swan-Clearwater summer range. Sanderson (1966) outlined 3 factors limiting home range sizes in animals that have been applied to summering white-tailed deer: (1) reduced mobility because of the constraints of young (Hawkins and Klimstra 1970, Gladfelter 1978, Ozoga *et al.* 1982); (2) social factors resulting from high population densities (Marchinton and Jeter 1966, Marshall and Whittington 1968, Smith 1970); and (3) high-quality habitat (Townsend and Smith 1933, Thomas *et al.* 1964, Marchinton and Jeter 1966, Sparrowe and Springer 1970). We did not address social factors, but they may have contributed to home range sizes and patterns we observed.

Deer in our study showed selection for both summer home range placement within the study area (2nd-order selection) and for use of specific habitats within those home ranges (3rd-order selection). The preference for riparian habitats may have been related to the abundance of high-quality forage located, the presence of free water, and

vegetative cover. Preference for riparian habitat for white-tailed deer has been documented elsewhere (Townsend and Smith 1933, Severinghaus and Cheatum 1956, Progulské and Duerre 1964, Allen 1968, Martinka 1968, Mundinger 1984).

The selection deer displayed for unlogged riparian habitat within their home ranges suggested that this was a preferred habitat category. Only 2 deer used logged riparian habitat more than expected, but their home ranges contained very little unlogged riparian habitat. Apparently, some preferred characteristics of riparian areas were still available following limited logging or habitat modification. However, unlogged riparian habitat appeared to be preferred when both logged and unlogged sites were available. In addition, as availability of unlogged riparian habitat increased, an individual's home range size decreased.

Deer used upland habitats less than expected, regardless of time of day (Leach 1982), abundance of upland habitats, or whether the stands were logged or unlogged. Our methods for detecting preferential habitat use may not have been sensitive to consistent albeit infrequent use of upland habitats. Johnson (1980) noted that time spent in a particular habitat does not always imply its value. Uplands, especially mature stands, no doubt have value for summering deer in the Swan-Clearwater area, but based on our results, the habitat values present in upland stands were of less importance to local deer than those found in riparian habitats.

Although adult deer did not select logged riparian habitat within their home ranges, this habitat category was important in home range establishment. Given fidelity of deer to home ranges, deer may be reluctant to relocate following logging activity in riparian habitats within their home range. Our results suggested that deer may have enlarged their summer home range as the ratio of logged to unlogged riparian habitat increased. Because home range location for female deer appears to be inherited, home range fidelity may have been established before the advent of logging. However, it was apparent that use of logged riparian habitat was highest where considerable deciduous cover and residual conifers remained following logging.

Home range distribution and use depends on social factors as well as habitat quality (Tierson *et al.* 1985). Adults and yearlings used habitats within their home ranges similarly, but there was evidence that yearling home ranges contained more

marginal habitat (less preferred) than did adult home ranges. Using adult habitat preferences as a standard for ranking, the order from most preferred to least preferred was: unlogged riparian, logged riparian, unlogged upland, and logged upland. Yearling deer occupied suboptimal habitats on our study area as did mule deer (*O. hemionus*) along the Missouri River Breaks of central Montana (Hamlin, Mont. Dept. Fish, Wildlife, and Parks, unpubl. data) and roe deer (*Capreolus capreolus*) in Denmark (Klein and Strandgaard 1972). This may have been the result of the dam's forcing yearlings out of preferred areas and naiveté of the yearlings.

Deer home ranges were located in areas with high habitat diversity where ecotones would be more common. Interspersion of diverse habitat types and riparian habitat polygons was common on deer ranges. Dahlberg and Guettinger (1956) and Progulské and Duerre (1964) stressed the importance of interspersion of openings and water as desirable components of deer summer range. Marchinton and Jeter (1966) concluded that the interspersion of foods changing in availability through time enabled deer to restrict movements to small home ranges.

Although our study did not evaluate the effects of specific silvicultural practices and forest management strategies on deer habitat, the following general guidelines seem warranted on deer summer range of the Swan-Clearwater. Riparian habitats, particularly unlogged ones, should be managed conservatively by establishing buffer zones of no logging. If logged, uneven-aged silvicultural systems should be used, to retain residual habitat. Quality upland cover should be maintained adjacent to riparian areas and other moist habitat components. A management goal should be habitat diversity on a small scale, accomplished with uneven-aged silviculture and prescribed fire. If even-aged management is applied, cutting unit size should be small (≤ 12 ha) and dispersed over the landscape. Postlogging scarification should be limited to the minimum necessary for successful conifer regeneration, to enhance shrub production for deer forage and cover.

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Great Basin Canada Goose Nesting on the Mid-Columbia River, Washington: An Historical Perspective and Update, 1981-1990

Abstract

Nesting of Great Basin Canada geese, *Branta canadensis moffiti*, on 20 islands in the Hanford Reach of the mid-Columbia River has been surveyed since 1953. Nest counts declined from over 300 in 1958 to a low of 108 in 1975. Since then, nest counts increased to a peak of 274 in 1989. The decline in 1960-1975 is attributed to the complete loss of Locke Island as nesting habitat caused by persistent coyote, *Canis latrans*, predation. In the early years, Locke Island alone accounted for 30 to 50% of the nests in the Hanford Reach. The increase in nest counts after 1975 reflects increasing nest density on islands downriver from Locke Island. Downriver islands were historically relatively free from coyotes. In 1989 and 1990, 70% of the nests were on five downriver islands near the city of Richland. The average annual nest count for 1981-1990 was 215. Eighty percent of the nests were successfully hatched. The occurrence of unsuccessful nests was attributed to depredation 8.4%, nest abandonment 7.7%, flooding 2.6%, and 0.5% of the unsuccessful nests had infertile eggs. These observations document year-to-year changes in the island nesting population of Canada geese along the last remaining unimpounded section of the Columbia River in the United States. Population changes are related to the changing environment, including coyote predation, in eastern Washington. These studies demonstrate the value of long-term monitoring in assessing environmental change.

Introduction

The nesting population of Great Basin Canada geese, *Branta canadensis moffiti*, along the mid-Columbia River on the U.S. Department of Energy Hanford Site (Hanford Reach) has been surveyed annually since 1953 (Hanson and Eberhardt 1971, Fitzner and Rickard 1983). This paper updates the survey by reviewing previous trends and providing new information obtained in the years 1981-1990. Prior to 1971, single-pass (once through) plutonium production reactors were operated along the Hanford Reach and released radionuclides into the Columbia River. Once the reactors were shutdown in early 1971, radionuclide concentrations in river water and biota declined (Cushing *et al.* 1981). Radionuclide concentrations in Canada goose eggs were very low in the years following reactor shutdown (Rickard and Sweany 1977, Rickard and Price 1990). Following reactor shutdown, recreational usage of the Columbia River increased, and regulated riverflows became more extreme. Woody vegetation, especially mulberry trees, *Morus alba*, and reed canary grass, *Phalaris arundinacea*, have flourished along the Hanford Reach shoreline (Fickeisen *et al.* 1980, Rickard *et al.* 1982). Dismantlement and cleanup of the old reactor areas is now a major mission of the Hanford Site. Surveys of the nesting performance of Canada geese provide information needed to evaluate population responses to a continually changing riverine environment.

Study Area

The Hanford Reach of the Columbia River extending upstream from Richland, Washington (Figure 1) is the only unimpounded river segment upstream from Bonneville Dam. The area contains 20 islands that historically have been used as nesting habitat by Great Basin Canada geese. Maps of each of the nesting islands with major vegetation types were presented by Dewaard (1981). Information on the ecology of Canada goose broods in the Hanford Reach were described in Eberhardt *et al.* (1989). Some of the islands have changed vegetatively since 1970, particularly Islands 18, 19, and 20, as a result of raised pool elevations of Lake Wallula, the impoundment created by McNary dam in 1955. Here, the establishment of tree and shrub willows, *Salix* spp., and rank herbaceous species rooted in soil and mud substrates; e.g., reed canary grass have replaced the sparse, shortstatured plant communities rooted in cobble stones and gravels which were adapted to the historical seasonal flooding regime of the free-flowing Columbia River (Fickeisen *et al.* 1980). Accelerated slumping of the White Bluffs initiated by irrigation water seepage from the Columbia Basin Irrigation project has shortened the riverine distance between Locke Island and the bluffs and Island 7 is now connected to the bluffs by a land bridge.

Methods

Islands were searched for goose nests by walking the length and breadth of each. Search team sizes

¹To whom reprint requests should be sent

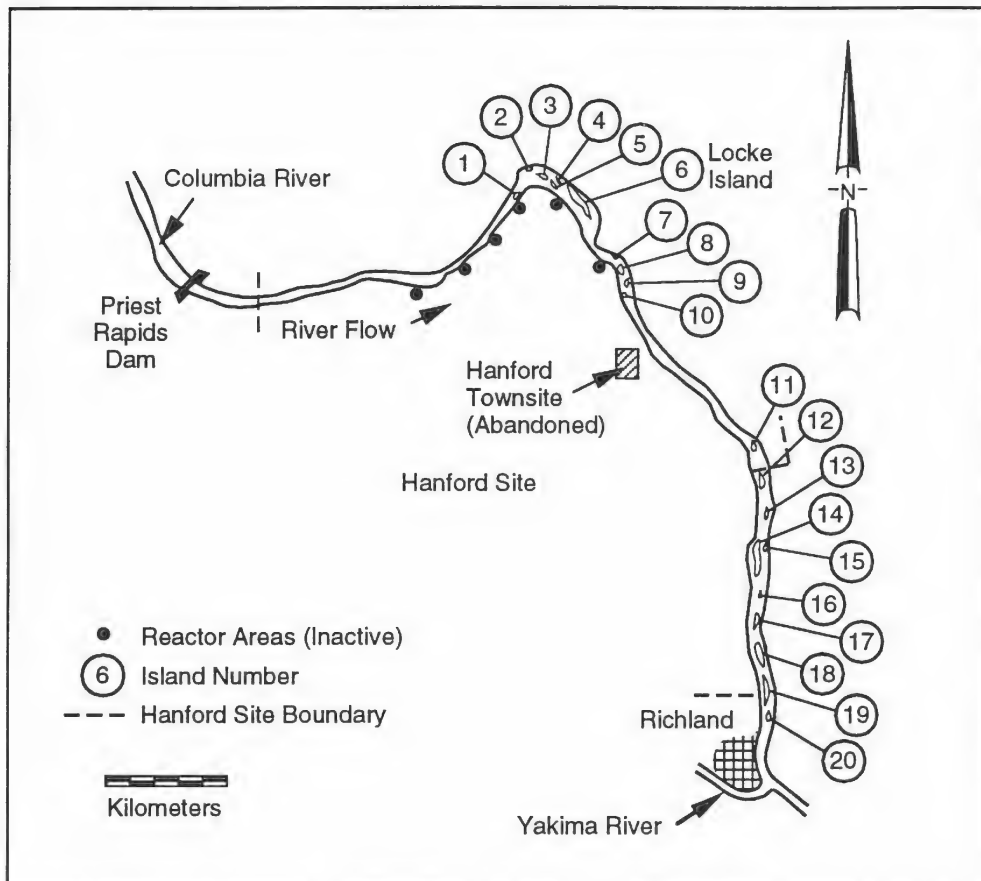


Figure 1. Map of the Columbia River upstream from Richland, Washington showing the distribution of 20 islands surveyed for goose nests. Upriver islands are numbered 1-10, downriver islands are numbered 11-20. Island number 6 is Locke Island.

varied but usually consisted of 2 to 6 persons. Each located nest was marked by an individually numbered willow wand stuck into the ground near the nest site. The location of each nest was described on a field data sheet with notes on substrate and dominant vegetation at each nest. The number of eggs in each nest was recorded. Nests were revisited at 10 to 14 day intervals. Searches were not made on days with inclement weather. A nest was judged to be successful if it contained the residues of egg shells with attached membranes characteristic of newly hatched eggs, filoplumes from natal down, pipped eggs or goslings. Unsuccessful nests were recorded as depredated, abandoned, flooded or as infertile. Eggs in abandoned

nests were broken to tell if they contained embryos. Surveys began the first week of April and continued until all nests were accounted for in May.

Results and Discussion

Results of goose nesting surveys for the ten-year period, 1981-1990, are summarized in Table 1. The average number of nests initiated yearly was 215. Numbers tended to increase towards the end of the study period. The lowest count of 166 nests was recorded in 1981 and the highest, 274, was recorded in 1989. The lowest nest count ever recorded was in 1975 when only 108 nests were recorded (Fitzner and Rickard 1983). Since the

TABLE 1. Productivity Measurements of Canada Goose Nests on Islands on the Hanford Reach of the Columbia River, 1981-1990

Year	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	Average
Total Nests	166	170	236	208	193	173	254	220	274	254	215
Number Successful Nests	144	141	155	147	161	160	193	176	226	205	171
% Successful Nests	87	81	66	71	83	92	76	80	82	81	79
Number Abandoned Nests	17	17	25	17	10	6	36	19	8	11	16.6 (7.7%)
Number Depredated Nests	11	11	38	30	18	0	12	25	24	12	18.1 (8.4%)
Number Flooded Nests	0	0	0	1	0	5	9	0	16	24	5.5 (2.6%)
Fate Undetermined Nests	9	2	12	8	0	0	4	0	0	2	3.7 (1.7%)
Infertile Nests	0	0	6	3	0	2	0	0	0	0	1.1 (0.5%)
Average Clutch Size	6.13	6.15	6.11	5.92	6.06	6.06	6.10	6.18	5.93	5.89	6.05

mid-1970s, nest counts have increased, approaching the peak levels recorded in the 1950s (Figure 2A).

The general decline in numbers of nests from 1959-1975 is attributed to severe coyote, *Canis latrans*, depredation on the 10 upriver islands (Figure 1). For example, in 1957, there were 129 nests on Locke Island. In 1959, coyotes destroyed all 96 nests (Hanson and Eberhardt 1971). Since 1970, coyotes have been persistent if not permanent dwellers on Locke Island making it unacceptable as nesting habitat. Although an active coyote suppression program was practiced along the Columbia River from 1970-1980, by agents of the Washington Department of Wildlife, coyotes still persisted on Locke Island (Fitzner and Rickard 1983). Fitzner and Rickard hypothesized that overall nest counts would not regain the high levels seen in the 1950s unless Locke Island was restored as nesting habitat. This hypothesis proved incorrect as the geese compensated by increasing nesting densities on downriver islands that historically were relatively free from coyote depredation (Figure 2B). In 1989 and 1990, 70% of the goose nests were on five of the downriver islands, 12, 17, 18, 19, and 20 (Figure 1). In the 1950s, Locke Island alone accounted for 30 to 50% of the total nests.

The reasons for high nest depredation by coyotes at upriver islands and fewer incidents on downriver islands are not well understood. Upriver islands are not open to waterfowl hunting during the annual October to January hunting season and,

therefore, serve as a refugium from shooting. The downriver islands, 11 to 18 are open to hunting and are heavily used by hunters. The presence of hunters may deter coyotes as the animals are vulnerable while swimming and are likely to be shot when seen on islands used for hunting. Islands 19 and 20 are located within the city limits of Richland where shooting is not allowed. Coyotes are rarely seen in this area of high public use. Distances between the shoreline and individual islands vary with changing water levels daily and seasonally as determined by hydroelectric power demands and availability of runoff in upriver watersheds. River flow and velocity and distance from an island to the river bank may be important factors in determining which islands are visited by coyotes. Unfortunately, little is known about the behavior of coyotes along the Columbia River.

Successful Nests

Although the numbers of nests initiated each year provides information concerning the abundance of nesting geese, the number of successfully hatched eggs indicates the number of young birds actually produced and an assessment of habitat quality. On average, 79.5% of the initiated nests successfully hatched. Only 66% and 71% of the nests initiated successfully hatched in 1983 and 1984, respectively. Increased human activity on the islands associated with a special study of brood ecology during these years (Eberhardt *et al.* 1987) may have been responsible, at least in part, for the

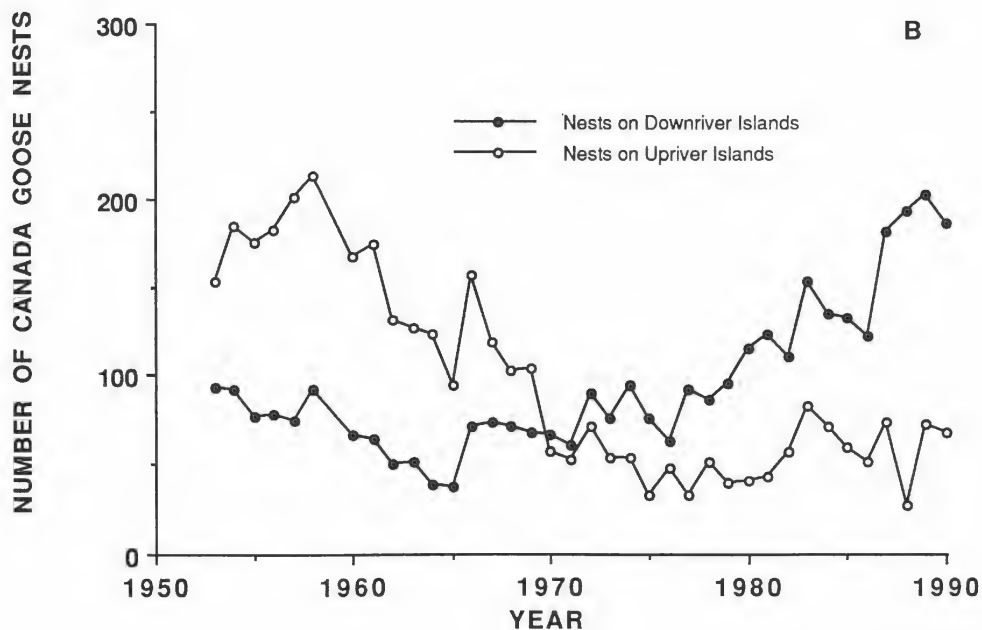
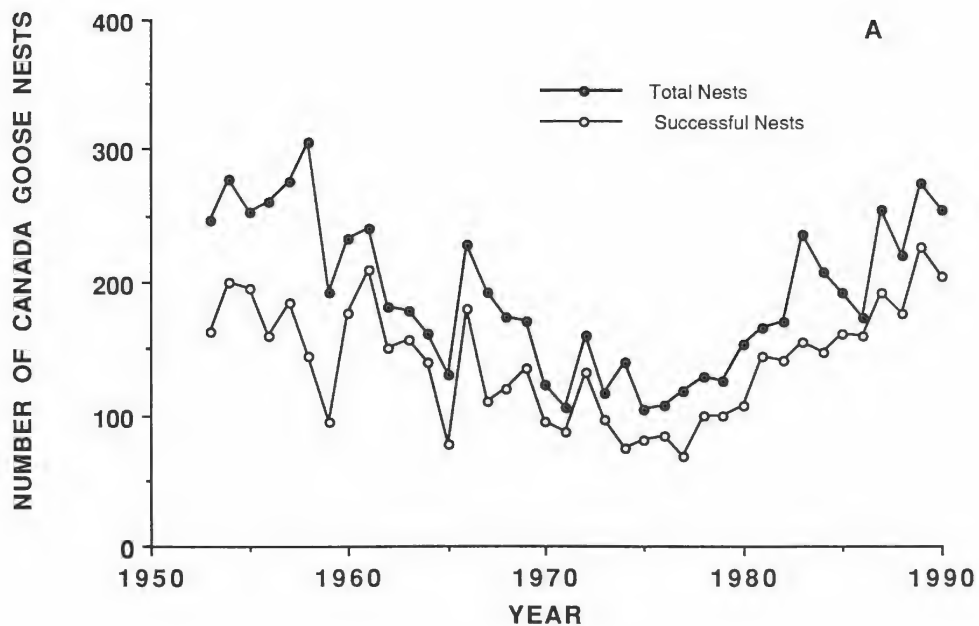


Figure 2. A) Total numbers of Great Basin Canada Goose nests initiated and successfully hatched on islands surveyed, 1953-1990. B) Total numbers of nests initiated on up- and downriver islands, 1953-1990.

lower hatching success. The 79.5% hatching success for the period 1981-1990 is higher than the 71% reported in 1950-1970 (Hanson and Eberhardt 1971) but is only slightly lower than the 82% reported in 1971-1981 (Fitzner and Rickard 1983). McCabe (1979) reported nesting success at 82% for Great Basin Canada geese nesting on the Umatilla National Wildlife Refuge on the Columbia River downriver from Richland. Ball *et al.* (1981) estimated nesting success statewide at 75%. Thus hatching success of Hanford Site nests is similar to other nesting areas in the state.

Unsuccessful Nests

Unsuccessful nests were classified as abandoned by the parent birds, destroyed by vertebrate predators, flooded by river water or failed to hatch because eggs were infertile (Table 1). A few nests were listed as undetermined because they could not be relocated. On average, 8.43% of unsuccessful nests were depredated, 7.74% abandoned, 2.56% flooded and 1.1% failed to hatch because they were not fertile (Table 1).

Although coyotes were responsible for most nest depredation observed in 1981-1990, common ravens, *Corvus corax*, and black-billed magpies, *Pica pica*, depredated some nests. In 1988, all 15 goose nests initiated on island 2 were depredated by ravens. A pair of ravens nested within 0.5 km of the island.

Nest losses to flooding were low during the first 8 years of the 1981-1990 survey period (Table 1). However, the average annual loss increased by a factor of 10 in 1989-1990. Whether or not nest losses by flooding will continue to increase remains to be seen. Nest losses to flooding were generally low in the 1950-1970 period but in 1956, 12% of the total nests were lost to flooding with most losses on upriver islands 2, 6, 8, and 9 (Hanson and Eberhardt 1971). In the 1980-1990 period, nest losses to flooding were mostly on downriver islands 18, 19, and 20.

Unsuccessful nests were abandoned by parent birds for various reasons including human visitations. Although the islands are posted with signs stating that human trespass is prohibited during the nesting season, these signs are not always heeded; for example in 1987, 36 nests were recorded as abandoned (Table 1). Most of these were on island 17. A fisherman accompanied by

a free-roaming dog were observed on the island early in the nesting season. This visitation and possibly others are believed to be at least partially responsible for the increased nest abandonment observed on island 17 in 1987.

Clutch Size

The number of eggs laid per nest reflects the reproductive potential of the nesting population. Over the years, average clutch size has increased from 5.5 in 1953-1970 to 5.6 in 1971-1981, and 6.05 in 1981-1990 (Table 1). The increased average clutch size during the past decade may indicate a higher quality environment associated with the shifting of the nesting population from upriver to downriver islands. More attention needs to be paid to this parameter in future studies.

Conclusions

This paper documents several decades of observations on the island nesting behavior and success of Canada geese in the last unpounded section of the Columbia River in the United States. Goose nesting has clearly shifted from upriver to downriver islands primarily in response to coyote predation. These observations demonstrate the value of long-term monitoring in assessing environmental change and may have implications in the development of management strategies for both predator and prey species.

Acknowledgements

On June 3, 1992, Richard E. Fitzner and Lester E. Eberhardt were killed in an airplane crash while conducting wildlife surveys. From 1970 through 1990, these men performed and supervised the annual goose nesting surveys on the Hanford Reach of the Columbia River. Their absence will be sorely missed. The long-term cooperation of U.S. Fish and Wildlife personnel from the McNary National Wildlife Refuge and biologists from the Washington Department of Wildlife during the goose surveys is greatly appreciated. The participation of many university students, and others that have helped in the surveys over the years is gratefully acknowledged. This work was supported by the U.S. Department of Energy under contract DE-AC06-76RLO 1830 with Battelle Memorial Institute.

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John H. Jerome and **Robert P. Bukata**, National Water Research Institute, Canada Centre for Inland Waters, Burlington, Ontario, Canada L7R 4A6

Paul H. Whitfield, Conservation and Protection, Environment Canada, North Vancouver, British Columbia, Canada V6M 3H7

and

Normand Rousseau, Environment Quebec, Saint Foy, Quebec, Canada

Colours of Natural Waters: 1. Factors Controlling the Dominant Wavelength

Abstract

The colour of natural water as perceived by the trichromatic response of the human eye is described in terms of dominant wavelength and purity. Chromaticity coordinates are discussed and a technique is presented for using such coordinates to determine the dominant wavelength and spectral purity of an upwelling irradiance spectrum observed over a natural water body. The principal factors influencing dominant wavelength and spectral purity (i.e. the observed aquatic colour) are the concentrations of the organic and inorganic materials comprising the water body. Optical cross sections (a quantification of scattering and absorption that can be attributed to a unit concentration of an organic or inorganic aquatic component) are utilized to illustrate the impacts of suspended organic, suspended inorganic, and dissolved organic matter on the dominant wavelengths and spectral purities of natural waters. It is shown that 1) low turbidity (i.e. simultaneously low concentrations of suspended minerals and chlorophyll) and low concentrations of dissolved organic carbon result in waters appearing blue to turquoise, 2) low turbidity and substantial concentrations of dissolved organic carbon result in waters appearing green to brown, and 3) high turbidity (i.e. high concentrations of suspended minerals and/or chlorophyll) or a high dissolved organic carbon concentration results in waters appearing brown in colour. With increasing concentrations, the dominant wavelength and spectral purity asymptotically approach constant values. Such "end-point" dominant wavelengths and "end-point" spectral purities are characteristic of all natural waters.

Introduction

The observed colour of a natural water body is a direct consequence of the interaction of the incident downwelling sky and solar irradiance with the optically-active organic and inorganic components of that water. The colour of water has often been considered to represent, in addition to one's initial aesthetic impression of the water, an indication of the quality of that water body. Indeed, as shown in great detail elsewhere (Bukata *et al.* 1981, 1985), determination of the degree of scattering and absorption per unit concentration of each of the principal organic and inorganic components of natural waters as a function of wavelength can enable direct measurements of the observed water colour to be used to estimate such water quality indicators.

Since water masses display both spatial and temporal variations in their organic and inorganic compositions, it logically follows that they will be characterized by related variabilities in their observed colour. Such colour variability is very much in evidence throughout inland lake and river systems, a direct consequence of the geological and vegetative diversity of the drainage basins and the impact of such diversity on the composition of associated natural waters.

It is the purpose of this paper to discuss this colour variability in terms of the specific absorption and scattering encountered in a variety of inland waters. To do so, optical cross section spectra recently reported in Bukata *et al.* (1991) will be utilized in conjunction with standard chromaticity analyses to illustrate the impact on perceived water colour of varying the co-existing concentrations of suspended minerals, chlorophyll, and dissolved organic carbon. The concepts of dominant wavelength and spectral purity will be briefly reviewed and applied to upwelling irradiance spectra.

In our companion paper (Jerome *et al.* 1994) we use the concepts of dominant wavelength, purity, and optical cross sections as developed in this paper to discuss the spectral colour variations observed in British Columbia river systems and to interpret such colour variations in terms of the elevation, drainage area, glacial-feed, groundwater intrusion, turbidity, and basin types defining the systems.

Direct Optical Measurements and Chromaticity Analyses

From the perspective of the human observer, colour is the effect of the interplay between the

light spectrum reaching the eye and the eye's spectral response. The human eye is trichromatic, i.e. it responds to the three spectral regions red, green, and blue. Thus, any perceived colour can be created by appropriately proportioning red, green, and blue light. Such apportionment of white light into its tristimulus red, green, and blue components forms the basis of chromaticity analyses.

Neglecting surface reflection (which can often mask a water's true colour), the colour of a natural water body is determined by its optical properties, particularly by the scattering and absorption coefficients which quantify the number of scattering and absorption events that photons undergo in their underwater propagation. The cumulative impact of such scattering and absorption events can be recorded by directly monitoring, as a function of wavelength λ , the subsurface volume reflectance $R(\lambda)$ (the ratio of upwelling irradiance $E_u(\lambda)$ to downwelling irradiance $E_d(\lambda)$ at a specified depth) throughout the visible spectral range (~ 380 -730 nm). The colour of light reflected back through the air/water interface can be obtained from the subsurface volume reflectance spectrum $R(\lambda)$, which, as shown by Jerome *et al.* (1988), is related to the scattering and absorption coefficients by the mathematical expressions

$$R(\lambda) = 0.319 \frac{B(\lambda)b(\lambda)}{a(\lambda)} \quad (1)$$

$$\text{for } 0 \leq \frac{Bb}{a} \leq 0.25$$

and

$$R(\lambda) = 0.267 \frac{B(\lambda)b(\lambda)}{a(\lambda)} + 0.013 \quad (2)$$

$$\text{for } 0.25 \leq \frac{Bb}{a} \leq 0.50$$

where a = absorption coefficient of the water body (m^{-1})
 b = scattering coefficient of the water body (m^{-1})
 B = backscattering probability of the water body.

The optical coefficients a , b , and B are generally controlled by three naturally-occurring aquatic components, viz. the dissolved organic matter, suspended organic matter, and suspended inorganic matter (in addition to the pure water itself). In general, dissolved inorganic matter does not influence the optical properties. The dissolved organic matter may be monitored by measuring the concentration of dissolved organic carbon (DOC), the suspended organic matter by measuring the

concentration of chlorophyll, and the suspended inorganic matter by measuring the concentration of suspended minerals.

If the specific contributions to spectral values $a(\lambda)$, $b(\lambda)$, and $B(\lambda)$ are known for each of the organic and inorganic aquatic components, then the volume reflectance of a water body containing any combination of these components can be predicted (Bukata *et al.* 1985, 1991). By incorporating this subsurface volume reflectance with a typical incident solar spectrum for a standard atmosphere such as discussed by Kneizys *et al.*, (1988) the upwelling light from the water may be calculated.

These measured/calculated upwelling irradiance spectra $E(\lambda)$ may then be related to a perception of visual colour through chromaticity analyses which integrate the sensitivity of the human eye with an impinging energy spectrum (Committee on Colorimetry, 1963). Such an integration produces tristimulus values X' , Y' and Z' , from which the chromaticity coordinates X (red), Y (green), and Z (blue) may be obtained.

Following the Committee Internationale Eclairage, CIE (Anonymous, 1957) standard colorimetric system the tristimulus values of an upwelling irradiance spectrum $E(\lambda)$ are given by

$$X' = \int E(\lambda) x(\lambda) d\lambda \quad (3)$$

$$Y' = \int E(\lambda) y(\lambda) d\lambda \quad (4)$$

$$Z' = \int E(\lambda) z(\lambda) d\lambda \quad (5)$$

where $x(\lambda)$, $y(\lambda)$, and $z(\lambda)$ are the CIE colour mixtures (for red, green and blue, respectively) for equal energy spectra and may be obtained from CIE tables (Jerlov, 1976).

The chromaticity coordinates X , Y , and Z (for red, green and blue, respectively) are then obtained from the equations

$$X = X' / (X' + Y' + Z') \quad (6)$$

$$Y = Y' / (X' + Y' + Z') \quad (7)$$

$$Z = Z' / (X' + Y' + Z') \quad (8)$$

Since $X + Y + Z = 1$, two chromaticity coordinates adequately represent colour in a chromaticity diagram. Consequently, the chromaticities in the ensuing discussions will be displayed as 2-dimensional plots of Y (green) and Z (blue).

Using the CIE colour mixture values, $x(\lambda)$, $y(\lambda)$, $z(\lambda)$ and assuming monochromatic light of a given wavelength as the spectrum $E(\lambda)$, the CIE chromaticity coordinates may be obtained for that

particular wavelength. By repeating this procedure, CIE chromaticity coordinates may be obtained for each wavelength throughout the visible spectrum. All the (Z, Y) pairs obtained in such a manner are plotted in Figure 1. The loci of these (Z, Y) pairs defines an envelope which encompasses all possible chromaticity values. For a "white" spectrum (i.e. $E(\lambda) = \text{constant}$) $X = Y = Z = 0.333$. This defines the achromatic colour or white point S illustrated in Figure 1. A numerical value of colour is then obtained by drawing a line from this white point S through the plotted chromaticity values of the measured spectrum (as indicated by the point C). The intersection of the line S-C with the curve envelope of Figure 1 (indicated by point L) specifies the dominant wavelength of the observed spectrum. It is this dominant wavelength that will be herein considered as the colorimetric definition of the natural water body.

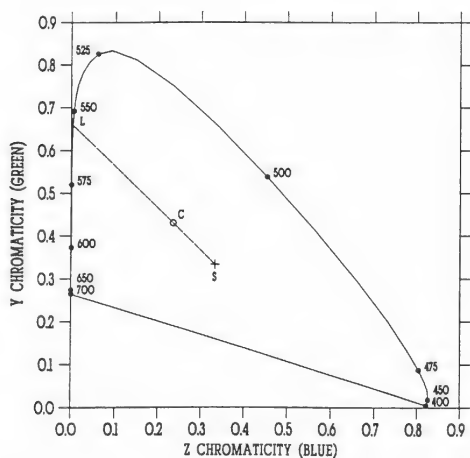


Figure 1. The Y (green) and Z (blue) CIE chromaticity coordinates appropriate for each wavelength throughout the visible spectrum. The white point S is shown for $Y = Z = 0.333$. The points C and L are as defined in the text.

The distinctiveness of this dominant wavelength is termed "purity" and is defined in Figure 1 as the ratio of the line C-S to the line L-S. Thus, spectral purity is a measure of the magnitude of the contribution of the dominant wavelength to an observed optical spectrum. A spectral purity of 1.0 indicates a monochromatic spectrum at the dominant wavelength, while a spectral purity of 0 indicates a "white" spectrum. Together, the dominant

wavelength and its associated spectral purity are considered herein as defining aquatic colour.

Influence of the Components of a Water Body on its Dominant Wavelength

The perceived colour of a natural water body is directly controlled by the scattering and absorption processes occurring within that natural water body. The direct linkages between the scattering and absorption and the measured subsurface volume reflectance spectra are the scattering and absorption coefficients per unit concentration of each aquatic component, i.e. the optical cross sections (Bukata *et al.* 1981). Optical cross sections are dependent upon the size, shape, composition and origin of the components of the aquatic regime. To obtain the required optical cross sections appropriate to a natural water body requires an integrated program of optical and water quality data collection, multiple regression, radiative transfer theory and optimization analyses which interweave in the manner discussed at length in Bukata *et al.* (1985). This type of large scale data collection and analyses program conducted in Lake Ontario (Bukata *et al.* 1981, 1991) has resulted in optical cross sections appropriate for the natural components of Lake Ontario. These optical cross-sections (determined for suspended minerals, chlorophyll, and dissolved organic carbon) may serve as a basis for explaining the variations in colour observed in lake and river waters.

As shown in equations (1) and (2) the subsurface volume reflectance $R(\lambda)$ can be determined from the backscattering and absorption coefficients $B(\lambda)b(\lambda)$ and $a(\lambda)$ appropriate to the water body under consideration. Further, $B(\lambda)b(\lambda)$ and $a(\lambda)$ may themselves be expressed in terms of the aquatic components, viz.

$$a(\lambda) = \sum a_i(\lambda) c_i \quad (9)$$

$$B(\lambda) b(\lambda) = \sum B_i(\lambda) b_i(\lambda) c_i \quad (10)$$

where $a_i(\lambda)$ and $B_i(\lambda) b_i(\lambda)$ represent the optical cross sections (i.e. the absorption coefficient and backscattering coefficient per unit concentration) of the i th aquatic component (including pure water) at wavelength λ , and c_i represents the concentration of the i th component.

Knowing the optical cross sections, therefore, enables the generation of a subsurface volume reflectance spectrum $R(\lambda)$ for any combination of

aquatic component concentrations. Once such $R(\lambda)$ are obtained, upwelling irradiance spectra $E(\lambda)$ may be readily generated upon which the CIE chromaticity analyses may be performed. Using Lake Ontario optical cross sections, dominant wavelengths were determined for various combinations of chlorophyll, suspended minerals and dissolved organic carbon. In this work the backscattering cross section for dissolved organic carbon is taken to be zero at all values of λ . The optical cross sections for pure water were taken from Smith and Baker (1981). The results of such theoretical analyses are depicted in Figures 2-4.

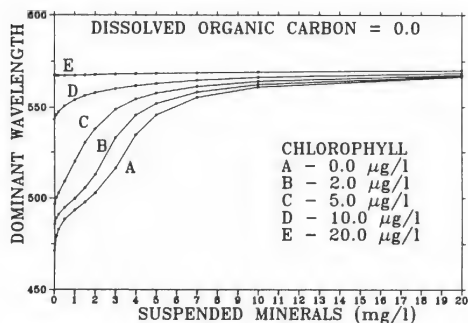


Figure 2. The family of relationships between dominant wavelength and suspended mineral concentration for a water mass in which the dissolved organic carbon concentration is kept fixed at zero while the concentration of chlorophyll is varied between 0 and 20 $\mu\text{g/l}$.

Figure 2 illustrates the family of relationships between dominant wavelength and suspended mineral concentration for a water mass in which the dissolved organic carbon is kept fixed at zero while the concentration of chlorophyll is varied between 0 and 20 $\mu\text{g/l}$. Figure 2 shows that low (470-500 nm) dominant wavelengths can be recorded for very low turbidity values. In the absence of chlorophyll and DOC, suspended mineral concentrations in the range 0-1.8 mg/l determine such dominant wavelength values. In the absence of suspended minerals and DOC, chlorophyll concentrations in the range 0-5.7 $\mu\text{g/l}$ determine such dominant wavelength values. Figure 2 also shows that high (>550 nm) dominant wavelengths can be recorded for moderate to high turbidity values. Values of suspended mineral > 5.7 mg/l result in high dominant wavelength values even in the absence of both chlorophyll and DOC. Similarly, concentrations of chlorophyll > 11.0 $\mu\text{g/l}$ result in high values of dominant wavelength even in the ab-

sence of both suspended mineral and DOC. Clearly evident from Figure 2 is the asymptotic approach of all curves to a common dominant wavelength value.

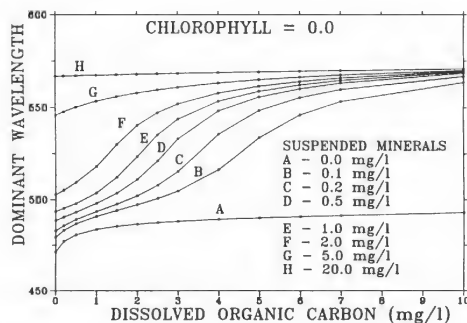


Figure 3. The family of relationships between dominant wavelength and dissolved organic carbon concentration for a water mass in which the chlorophyll concentration is kept fixed at zero while the concentration of suspended minerals is varied between 0 and 20 mg/l.

Figure 3 illustrates the family of relationships between dominant wavelength and dissolved organic carbon concentration for a water mass in which the chlorophyll concentration is kept fixed at zero while the concentration of suspended mineral is varied between 0 and 20 mg/l. It is interesting to note that in the absence of suspended mineral and chlorophyll concentrations (Curve A), the dominant wavelength remains relatively unaltered despite the amount of DOC present in the water. This is a consequence of the fact that for the conditions of Curve A the only backscattering is due to the water itself. DOC affects aquatic colour only through absorption. Curve B illustrates that the addition of a small amount of suspended mineral (and therefore the addition of particulate scattering centres to the water) accentuates the impact on dominant wavelength of increasing or decreasing DOC concentrations. Inland waters rarely, if ever, are characterized by the total absence of particulate scattering centres (i.e. suspended mineral concentration will never be 0.0). Consequently, the probability of observing the theoretical relationship of Curve A is exceedingly small. The lower limit relationship of dominant wavelength versus DOC observed for natural waters will therefore lie somewhere between Curves A and B. Also evident from Figure 3 is the association of low values of dominant wavelengths with low

concentrations of suspended minerals and DOC, and high values of dominant wavelengths with moderate to high concentrations of suspended minerals.

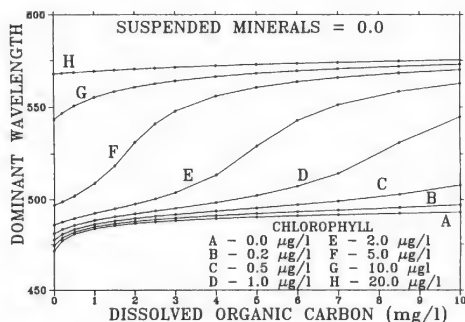


Figure 4. The family of relationships between dominant wavelength and dissolved organic carbon concentration for a water mass in which the suspended mineral concentration is kept fixed at zero while the concentration of chlorophyll is varied between 0 and 20 µg/l.

Figure 4 illustrates the family of relationships between dominant wavelength and dissolved organic carbon concentration for a water mass in which the suspended mineral concentration is kept fixed at zero while the concentration of chlorophyll is varied between 0 and 20 µg/l. The role of chlorophyll concentrations in accentuating the impact of DOC on dominant wavelength is similar to the role of suspended mineral in this regard. Again this is because the presence of chlorophyll (i.e., algal cells) contributes particulate scattering centres to a water mass that would otherwise be devoid of such scattering centres. An asymptotic approach to a common value of dominant wavelength is not as readily apparent in Figure 4 as it is in Figure 3. A chlorophyll concentration of ~2.0 µg/l (Figure 4, Curve E) is required before the asymptotic approach is clearly evident. This can be compared to a suspended mineral concentration of ~0.1 mg/l (Figure 3, Curve B), suggesting that ~0.1 mg/l of suspended minerals provides an optical impact comparable to that provided by ~2.0 µg/l of chlorophyll.

For completeness, Figure 5 illustrates the family of relationships between dominant wavelength and chlorophyll concentration for a water mass in which the DOC concentration is kept fixed at zero while the concentration of suspended mineral is varied between 0 and 20 mg/l. The similarity of

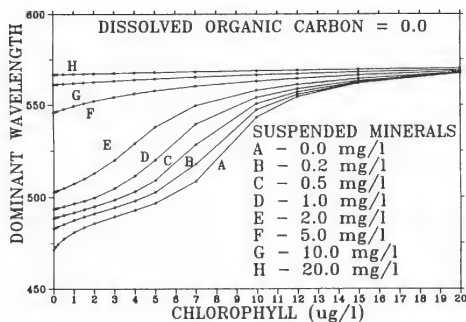


Figure 5. The family of relationships between dominant wavelength and chlorophyll concentration for a water mass in which the dissolved organic carbon concentration is kept fixed at zero while the concentration of suspended mineral is varied between 0 and 20 mg/l.

Figure 5 to Figure 2 is readily apparent, emphasizing the optical competitiveness of chlorophyll and suspended mineral in determining water colour. With respect to the dominant wavelengths that natural waters would exhibit, Figures 2-5 illustrate that:

1. "Pure water" displays a dominant wavelength of ~471 nm. This can be compared with oceanic values of 470-473 nm for near-surface upwelling irradiance reported in Jerlov (1976).
2. Low turbidity (i.e. simultaneously low concentrations of suspended mineral and chlorophyll) will result in upwelling irradiance spectra $E(\lambda)$ characterized by low values of dominant wavelengths, provided the dissolved organic carbon concentration is also low.
3. Low turbidity waters may, however, display upwelling irradiance spectra characterized by high values of dominant wavelengths if substantial concentrations of dissolved organic carbon are present.
4. High turbidity or high DOC concentrations result in high values of dominant wavelengths. The analyses indicate asymptotic values of ~580 nm as upper limits for dominant wavelengths for waters comparable to those comprising Lake Ontario. This implies that an "end-point" dominant wavelength will be displayed by any natural water mass once some value of turbidity is exceeded. This turbidity could be a consequence of solely organic, solely inorganic, or some combination of organic and inorganic materials. Such an "end-point" aquatic colour appears to be defined by dominant wavelengths in the green/red transition region of the visible spectrum.

As a further illustration of the development of this "end-point" aquatic colour, Figures 6 and 7 display the inter-relationships among dissolved organic carbon, chlorophyll, and suspended mineral concentrations and dominant wavelength for a pair of inland water types. Figure 6 illustrates the contour diagram of dominant wavelengths resulting from water masses comprised of various combinations of co-existing suspended mineral and chlorophyll concentrations, but for which the DOC concentration is kept fixed at 2.0 mg/l [which, as reported in Bukata *et al.*, (1981) is a reasonable typical value for the lower Great Lakes]. It is evident from Figure 6 that low values of turbidity (i.e., simultaneously occurring low chlorophyll and low suspended mineral concentrations) result in low values of dominant wavelength. It is also evident that while any concentration of chlorophyll or suspended mineral can be associated with any of the contoured dominant wavelengths, only specific ranges of co-existing concentrations of chlorophyll and suspended mineral will result in a specific

aquatic colour (for a fixed DOC concentration). The most evident feature of Figure 6, however, is that increasing the concentrations of suspended minerals and/or chlorophyll (i.e., individually or collectively) will result in the attainment of an "end-point" dominant wavelength.

Figure 7 illustrates the contour diagram of dominant wavelengths resulting from water masses comprised of various combinations of co-existing suspended mineral and DOC concentrations, but for which the chlorophyll concentration is kept fixed at 3.0 $\mu\text{g/l}$. Figure 7 can, therefore, be considered to represent an often-encountered situation in rivers wherein suspended sediment and dissolved organics are the aquatic colour determinants. The similarities of Figures 6 and 7 are indeed striking, and together illustrate that increasing the concentrations of suspended minerals, chlorophyll, and/or DOC (singularly or in tandem) will result in natural waters asymptotically approaching similar "end-point" dominant wavelengths.

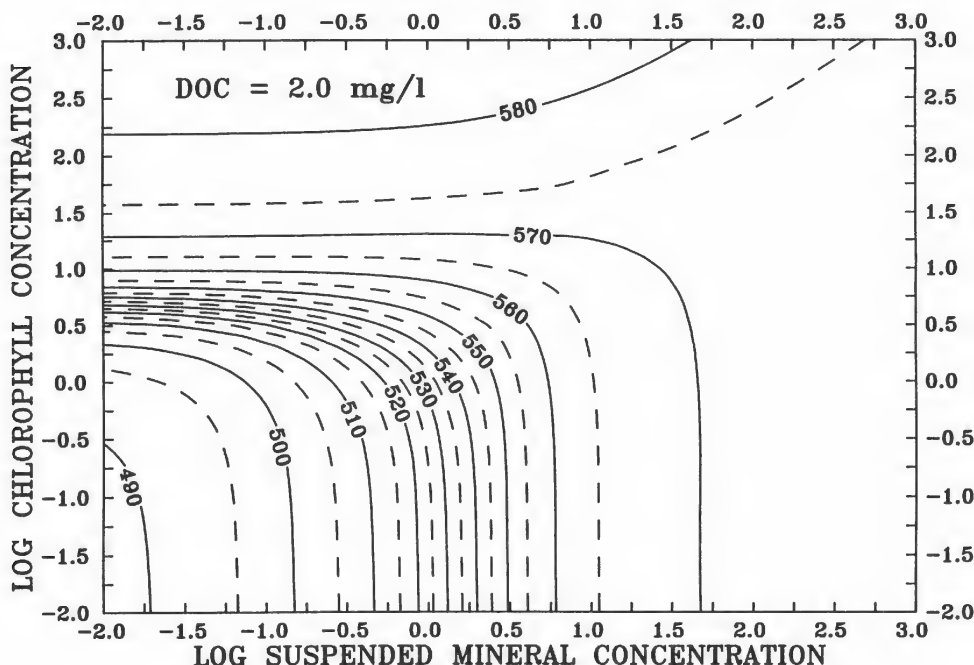


Figure 6. Contour diagram of dominant wavelengths resulting from various combinations of co-existing concentrations of chlorophyll and suspended minerals in a water mass containing a fixed dissolved organic carbon concentration of 2.0 mg/l.

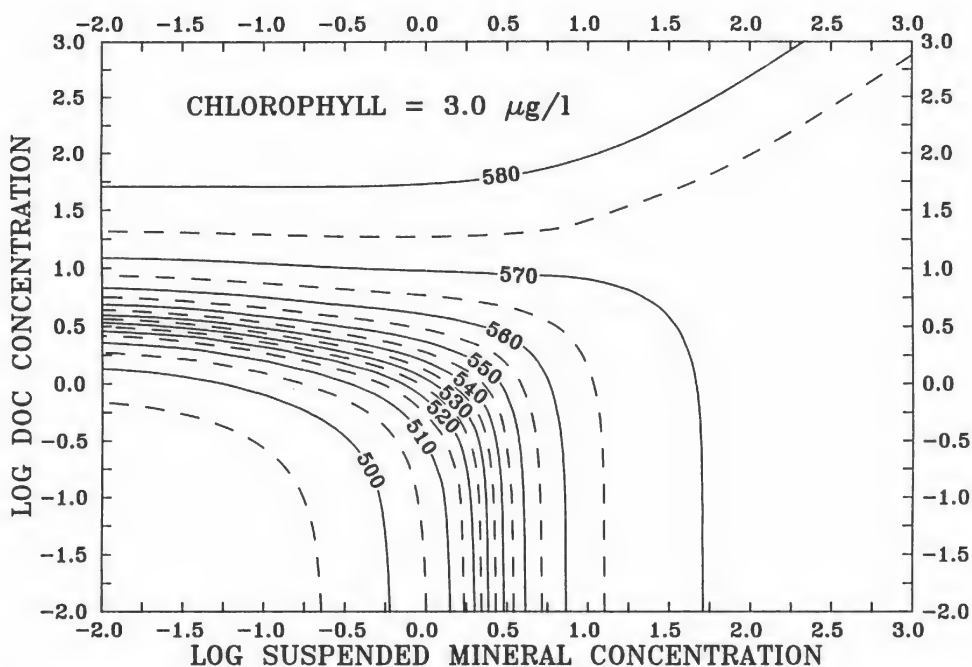


Figure 7. Contour diagram of dominant wavelengths resulting from various combinations of co-existing concentrations of suspended minerals and dissolved organic carbon in a water mass containing a fixed chlorophyll concentration of $3.0 \mu\text{g/l}$.

Influence of the Components of a Water Body on its Spectral Purity

Figure 8 illustrates the relationships between spectral purity and suspended mineral concentration for a water mass in which the dissolved organic carbon concentration is kept fixed at zero while the chlorophyll concentration assumes the values of 0, 1.0, and $10.0 \mu\text{g/l}$, respectively. Curve A (a water mass containing no chlorophyll and no DOC) shows that the spectral purity of "pure water" rapidly decreases with the intrusion of a small concentration of suspended mineral. However, once a suspended mineral concentration of $\sim 3 \text{ mg/l}$ is exceeded, the suspended minerals become a dominant aquatic colour determinant, and the spectral purity asymptotically increases. Curve B shows that as the chlorophyll concentration increases, the minimum of the relationship shifts to lower concentrations of suspended minerals. At sufficiently large chlorophyll concentrations (Curve C) the minimum disappears from the relationship, and only the asymptotic approach to an "end-point" spectral purity is displayed.

Figure 9 illustrates the relationships between spectral purity and chlorophyll concentration for a water mass in which the suspended mineral concentration is kept fixed at zero while the DOC concentration assumes the values 0, 1.0, and 10.0 mg/l , respectively. A similar progression of relationships is evident from Figure 9 as is evident in Figure 8. In this situation, however, the asymptotic approach to an "end-point" spectral purity is not as rapidly established.

Figure 10 illustrates the relationships between spectral purity and dissolved organic carbon concentration for a water mass in which the chlorophyll concentration is kept fixed at zero while the suspended mineral concentration assumes the values 0, 1.0, and 10.0 mg/l , respectively. In the absence of particulate scattering centres (Curve A), no reversal in the decreasing spectral purity occurs as the "end-point" spectral purity is asymptotically approached. This "end-point" spectral purity is significantly different from the "end-point" spectral purity for water bodies containing particulate scattering centres (Curves B and C). Curves B and C

display the progression of relationships observed in Figures 8 and 9.

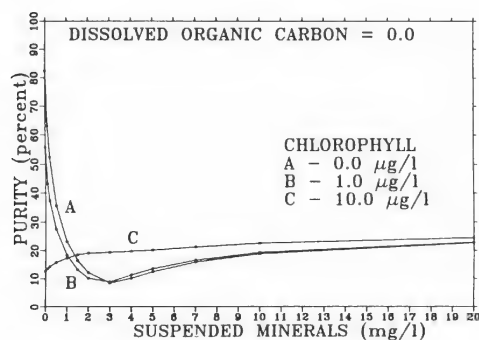


Figure 8. The family of relationships between spectral purity and suspended mineral concentration for a water mass in which the dissolved organic carbon concentration is kept fixed at zero while the chlorophyll concentration assumes the values 0, 1.0, and 10.0, respectively.

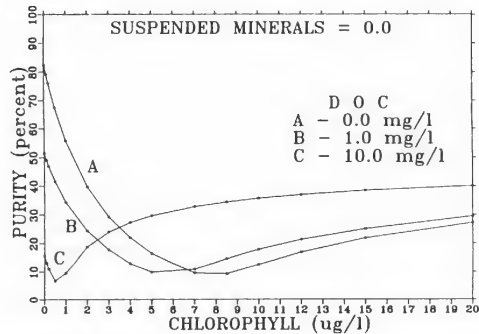


Figure 9. The family of relationships between spectral purity and chlorophyll concentration for a water mass in which the suspended mineral concentration is kept fixed at zero while the dissolved organic carbon concentration assumes the values 0, 1.0, and 10.0, respectively.

With respect to the spectral purity defining the perceived colour of natural waters, Figures 8-10 illustrate that:

1. "Pure water" displays a spectral purity (~82%) considerably higher than even the least turbid of natural waters. This compares favourably with observed oceanic purity values of 81-87% for near-surface upwelling irradiance reported in Jerlov (1976).
2. The intrusion of suspended minerals or chlorophyll into "pure water" results in rapid deteri-

oration of the spectral purity until some concentration of the added component is attained. Beyond that concentration, the aquatic component ceases to be a disruptive spectral purity influence and becomes a dominant colourant. This manifests as an asymptotic approach to an "end-point" spectral purity.

3. The spectral purity of a water body containing solely a high concentration of DOC is significantly increased by the intrusion of chlorophyll or suspended minerals into the system. This is largely a consequence of the suspended organic and inorganic matter adding particulate scattering centres to the water.
4. While the aquatic components may (at least for Lake Ontario-type waters) ultimately generate "end-point" dominant wavelengths that are numerically similar, they would not ultimately generate "end-point" spectral purities that display a corresponding numerical similarity.

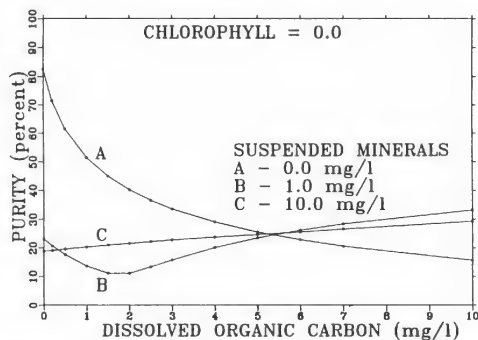


Figure 10. The family of relationships between spectral purity and dissolved organic carbon concentration for a water mass in which the chlorophyll concentration is kept fixed at zero while the suspended mineral concentration assumes the values 0, 1.0, and 10.0, respectively.

Extending the chromaticity analyses to obtain numerical estimates of "end-point" dominant wavelengths and spectral purities, concentrations of 1000 µg/l for chlorophyll and 1000 mg/l for suspended minerals and DOC were utilized in conjunction with the Lake Ontario optical cross sections. The results of these "end-point" aquatic colour determinations are listed in Table 1. The "end-point" dominant wavelengths are seen to be quite similar, ranging from 572-583 nm for any combination of high concentrations of chlorophyll, suspended minerals, and DOC. The "end-point"

TABLE 1. Estimates of "end-point" aquatic colours

Chlorophyll Concentration (µg/l)	Suspended Mineral (mg/l)	DOC Concentration (mg/l)	Dominant Wavelength (nm)	Spectral Purity (%)
0	0	0	471	83
0	0	1000	578	10
0	1000	0	572	27
1000	0	0	582	48
1000	0	1000	583	55
0	1000	1000	576	35
1000	1000	0	574	30
1000	1000	1000	576	37

spectral purities, however, are seen to be quite dissimilar, ranging from 10-55% (exclusive of "pure water").

Concluding Remarks

The perceived colour of a natural water body has been discussed in terms of 1) the trichromatic response of the eye, 2) the relationships among the subsurface volume reflectance, upwelling irradiance, and scattering and absorption cross sections, and 3) the relationships among the dominant wavelengths and spectral purities of observed upwelling spectra and the composition of natural waters in terms of the co-existing concentrations of chlorophyll, suspended minerals, and dissolved organic carbon.

Using optical cross section values appropriate to Lake Ontario, it was shown that natural waters display a range of dominant wavelengths which are dictated by the organic and inorganic compositions of the waters. Table 2 illustrates this range of observable dominant wavelengths, along with the con-

centrations of chlorophyll, suspended minerals, and DOC which are required to produce those dominant wavelengths. Two types of entries are listed for the low dominant wavelength values (470 nm–500 nm). Ranges of concentration values of each of chlorophyll, suspended minerals, and DOC are listed which would, in the absence of the other two components, display low values of dominant wavelength. Also included is an entry which considers a water mass that contains no chlorophyll but DOC and a very small concentration (0.1 mg/l) of suspended minerals. As discussed earlier, this entry is intended to illustrate a realistic estimate of the lower dominant wavelength/DOC relationship (Curve A of Figure 3) that would be appropriate for many natural waters. Since most natural waters contain at least some foreign scattering centres, the range of DOC values listed for a suspended mineral concentration of 0.1 mg/l is presented as an illustration of such waters. The entries for the high range of observable dominant wavelengths (550–585 nm) are minimal concentrations of chlorophyll,

TABLE 2. Concentrations of chlorophyll, suspended minerals, and dissolved organic carbon related to dominant wavelength ranges

Dominant Wavelength Range (nm)	Chlorophyll Concentration (µg/l)	Suspended Mineral (mg/l)	DOC Concentration (mg/l)
470-500	0 ≤ Chl ≤ 5.7	0	0
	or 0	0 ≤ SM ≤ 1.8	0
	or 0	0	0 ≤ DOC ≤ 24.0
	or 0	0.1	0 ≤ DOC ≤ 2.4
550-585	Chl ≥ 11.0		
	or	SM ≥ 5.7	
	or		DOC ≥ 58.2
	or	0.1	DOC ≥ 6.5

suspended minerals, and DOC which, if present in a natural water mass, will result in high dominant wavelength values irrespective of the concentrations of the other two components. Again, to allow for the high probability that every natural water mass contains at least some scattering centres, an entry for a water mass containing DOC and a small concentration (0.1 mg/l) of suspended minerals is also included.

Asymptotic upper limits to dominant wavelength and spectral purity of natural waters have resulted from the use of optical cross sections appropriate to Lake Ontario. Optical cross sections, understandably, display spatial and temporal variations as they are a consequence of the types of suspended and dissolved organic and inorganic materials indigenous to a specific water body. While the use of optical cross sections appropri-

ate to waters other than Lake Ontario will undoubtedly result in asymptotic upper limits of dominant wavelength and spectral purity different from those of Lake Ontario, asymptotic limits will, nonetheless, arise. Such "end-point" aquatic colour is attainable in any of three possible ways: 1) high concentrations of suspended mineral, 2) high concentrations of chlorophyll, or 3) low concentrations of suspended mineral coupled with high concentrations of dissolved organic materials.

Expressed simply, high turbidity waters ultimately display brownish colours, irrespective of whether the source of such turbidity is organic or inorganic in nature. Low turbidity waters display bluish colours to the human eye, although the presence of substantial concentrations of dissolved organic material can cause such low turbidity waters to appear green or brown to the human eye.

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John H. Jerome and **Robert P. Bukata**, National Water Research Institute, Canada Centre for Inland Waters, Burlington, Ontario, Canada L7R 4A6

Paul H. Whitfield, Conservation and Protection, Environment Canada, North Vancouver, British Columbia, Canada V6M 3H7

and

Normand Rousseau, Environment Canada, Saint Foy, Quebec, Canada

Colours of Natural Waters: 2. Observations of Spectral Variations in British Columbia Rivers

Abstract

Subsurface volume reflectance spectra in the range 400-740 nm were directly measured on four separate occasions at each of fourteen river stations in British Columbia during 1986 and 1987. Chromaticity analyses were performed on volume reflectance spectra to define aquatic colour in terms of a dominant wavelength and its associated purity. An attempt was made to explain water colour variations in British Columbia river systems based upon elevation, drainage area, glacial-feed, groundwater intrusion, turbidity, and basin type. It is shown that simple sub-basins which are glacier-fed and meltwater-dominated generally display dominant wavelengths in the interval 480-550 nm (i.e. colours usually perceived to be in the range blue to turquoise to green), a consequence of low to moderate turbidity comprised predominantly of suspended inorganics. Simple sub-basins which are non glacier-fed and groundwater-dominated display dominant wavelengths in the interval 550-570 nm (i.e. colours perceived to be in the range green to brown), a consequence of low to high particulate turbidity in conjunction with substantial concentrations of dissolved organics. Most of the large river basins of the Canadian Cordillera are comprised of a complex of sub-basins, and thus represent the integration of inputs from several sources. These complexes are shown to display dominant wavelengths in the restricted wavelength interval 573-578 nm. Such an "end-point" dominant wavelength causes the river water to be perceived as brownish in colour.

Introduction

In our companion paper (Jerome *et al.* 1994) we have described how the observed colour of a natural water body (in terms of the dominant wavelength of its upwelling irradiance spectrum) is a direct consequence of the absorption and scattering properties (as a function of wavelength) that may be confidently ascribed to a unit concentration of each of the principal organic and inorganic components of that water body.

Natural water masses, particularly those strongly influenced by the proximity of land masses, display both spatial and temporal variations in their organic and inorganic compositions. Consequently, they will be characterized by related variabilities in their associated dominant wavelengths. Such colour variability is exhibited throughout the British Columbia river systems. This is a result of the geological and vegetative diversity characterizing the Canadian Cordillera and the impact of such diversity on the composition of associated natural water bodies.

This paper presents the results of an optical survey of British Columbia river stations taken during 1986 and 1987. An attempt to quantify the visual colour of natural water in terms of the human eye's spectral response is discussed, as are

possible explanations for the visual colour variations defining the British Columbia river systems.

Sampling Stations

Figure 1 illustrates the location of the fourteen sampling stations used in the current survey. All stations are river-based and all form part of a network of sampling stations in southern British Columbia operated under the auspices of the Inland Waters Directorate of Environment Canada. Also shown in Figure 1 are the drainage basins for the surveyed rivers.

Subsurface volume reflectance (the ratio of upwelling irradiance to downwelling irradiance at a specified depth) spectra were determined at each station throughout the spectral range 400-740 nm utilizing a Techtron QSM 2500 scanning Quantaspectrometer. Each station was visited twice a year during 1986 and 1987, once in early summer and once in autumn, the intention being to sample at or near both peak and minimum flow rates. Table 1 lists the rivers, station locations (station numbers as shown in Figure 1), sampling dates, station elevations, and river flow rates for the station or a nearby station.

In addition to the subsurface optical spectra obtained at each station, water samples were collected to obtain concentrations of turbidity.

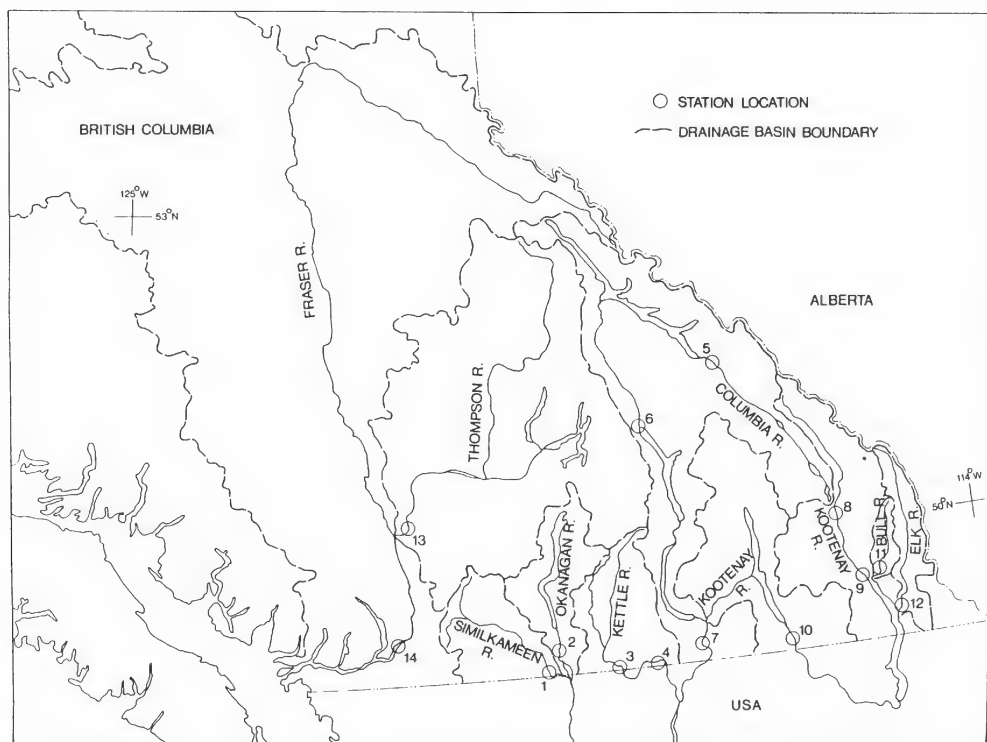


Figure 1. British Columbia river sampling stations.

In this study the optical measurements were performed *in situ* to eliminate the effects of surface reflection and to directly measure the subsurface volume reflectance of the water $R(\lambda)$. These $R(\lambda)$ spectra were then combined with an incident radiation spectrum for a standard atmosphere taken from Kneizys *et al.* (1988), to obtain an upwelling irradiance spectrum $E(\lambda)$ for each station and each sampling date.

Volume Reflectance Spectra of British Columbia River Waters

Subsurface volume reflectances were measured twice a year during 1986 and 1987 for the fourteen river stations listed in Table 1. Large variations in both magnitude and spectral shapes were observed. These variations are illustrated in Figure 2 which displays the summer and fall subsurface volume reflectance spectra recorded at stations 3 (Kettle River at Midway), 6 (Columbia River at Revelstoke), 8 (Kootenay River at Canal Flats), and 14 (Fraser River at Hope). Measured values of sub-

surface volume reflectance of British Columbia river water ranged from as low as $\sim 3\%$ to as high as 15-20%

The subsurface volume reflectance spectra reported here were obtained at different local times during different Julian days. Consequently, incident radiation distributions resulting from various combinations of solar and sky irradiances were encountered. The volume reflectance spectra have not been normalized to, say, vertical sun angles and standard sky irradiance. Such normalization would certainly impact the magnitude of $R(\lambda)$ (up to a maximum of $\pm 25\%$ of the measured value) but would not impact the spectral shape of $R(\lambda)$. Normalization is, therefore, unessential to chromaticity analyses of subsurface volume reflectance.

Dominant Wavelengths of British Columbia River Waters

Using measured volume reflectance spectra and an incident radiation spectrum for a standard clean, dry atmosphere taken from Kneizys *et al.* (1988),

TABLE 1. British Columbia River sampling locations and dates.

Station Number	River and Location	Drainage Area km ²	Mean Annual Discharge (m ³ /s)	Station Elevation (m)	Sampling Dates	Flow Rate (m ³ /s)
1	Similkameen River	9180	65.2	365	15 June 1986	199
					29 Sept 1986	17
					22 June 1987	80
					20 Oct 1987	7
2	Okanagan River at Oliver	7590	17.6	305	15 June 1986	37
					29 Sept 1986	14
					22 June 1987	7
					20 Oct 1987	11
3	Kettle River at Midway	5750	43	550	15 June 1986	97
					30 Sept 1986	14
					23 June 1987	28
					20 Oct 1987	3
4	Kettle River at Gilpin	9840	82	520	15 June 1986	178
					30 Sept 1986	22
					23 June 1987	61
					20 Oct 1987	5
5	Columbia River at Donald	9710	174	785	2 Oct 1986	91
					25 June 1987	437
					22 Oct 1987	50
6	Columbia River at Revelstoke	26700	854	425	2 Oct 1986	1390
					25 June 1987	
					22 Oct 1987	
7	Columbia River at Trail	155000	2830	415	15 June 1986	2080
					23 June 1987	1840
					20 Oct 1987	1510
8	Kootenay River at Canal Flats	5390	87.2	810	1 Oct 1986	56
					24 June 1987	150
					21 Oct 1987	28
9	Kootenay River at Fenwick Station	13600	205	755	16 June 1986	642
					1 Oct 1986	91
					24 June 1987	305
					21 Oct 1987	49
10	Kootenay River at Creston	35500	449	545	16 June 1986	411
					30 Sept 1986	232
					23 June 1987	197
					21 Oct 1987	597
11	Bull River at Hatchery	1530	32.9	755	16 June 1986	70
					1 Oct 1986	18
					24 June 1987	36
					21 Oct 1987	7
12	Elk River at Highway #93	4450	75.7	700	16 June 1986	132
					1 Oct 1986	26
					24 June 1987	59
					21 Oct 1987	14
13	Thompson River at Spences Bridge	54900	775	225	3 Oct 1986	388
					25 June 1987	1740
					23 Oct 1987	211
14	Fraser River at Hope	217000	2720	45	16 June 1986	10300
					29 Sept 1986	1410
					22 June 1987	5760
					19 Oct 1987	912

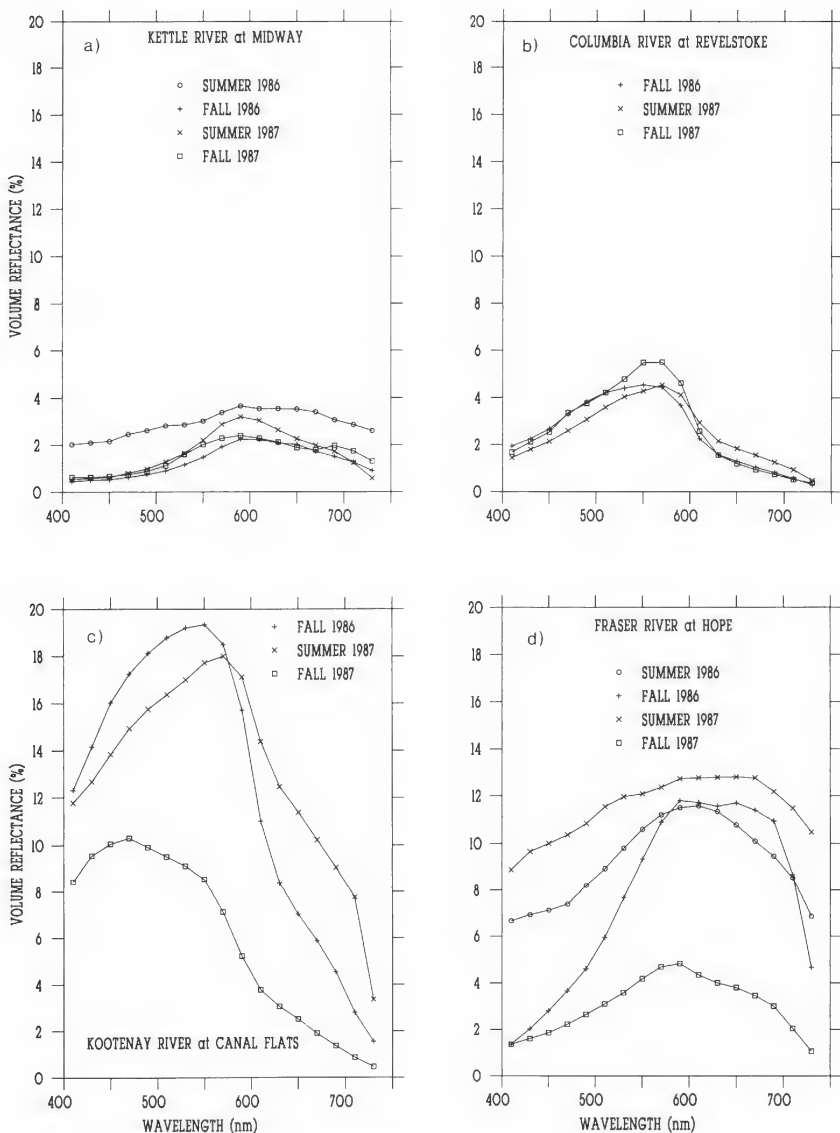


Figure 2. (a) Subsurface volume reflectance spectra recorded at Station 3 (Kettle River at Midway). (b) Subsurface volume reflectance spectra recorded at Station 6 (Columbia River at Revelstoke). (c) Subsurface volume reflectance spectra recorded at Station 8 (Kootenay River at Canal Flats). (d) Subsurface volume reflectance spectra recorded at Station 14 (Fraser River at Hope).

upwelling irradiance spectra were obtained for each station and sampling date. Chromaticity coordinates for each upwelling spectra were then calculated in the manner described in our companion paper (Jerome *et al.* 1994). Figures 3 and 4 illus-

trate chromaticity plots for stations 4 (Kettle River at Gilpin) and 14 (Fraser River and Hope), respectively. Also shown on Figures 3 and 4 are the white point S and the curve envelope. From the chromaticity plots the dominant wavelengths along with

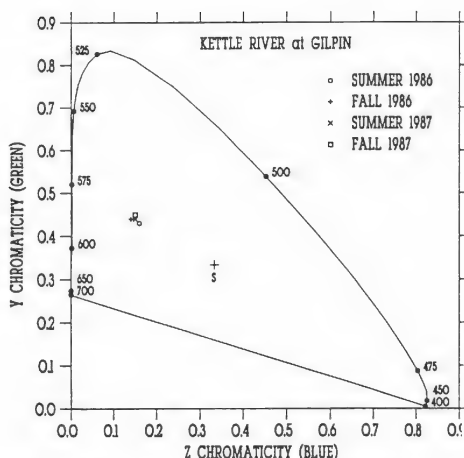


Figure 3. Chromaticity coordinate values for Station 4 (Kettle River at Gilpin).

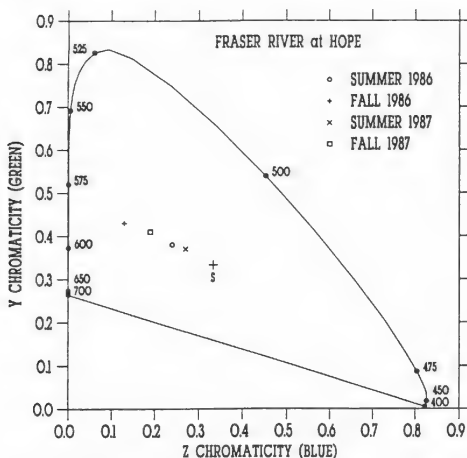


Figure 4. Chromaticity coordinate values for Station 14 (Fraser River at Hope).

their purity were determined for each upwelling spectrum for each station and each visit. An analysis of all fourteen stations showed that:

- 1) The points for a station may be closely clustered, e.g. Kettle River at Gilpin (station 4) and Columbia River at Trail (station 7). These stations display comparable dominant wavelengths and comparable purities.
- 2) The points for a station may be positioned along a line extending from the white point to the enveloping curve, e.g. Kettle River

at Midway (station 3) and Fraser River at Hope (station 14). These stations display comparable dominant wavelengths but non-comparable purities.

- 3) The points for a station may be non-clustered, e.g. Kootenay River at Canal Flats (station 8) and Bull River at the Hatchery (station 11). These stations display non-comparable dominant wavelengths and non-comparable purities.

All the calculated dominant wavelengths and purity values are listed in Table 2. Two sets of entries are given for each station, namely the dominant wavelengths and purities observed in the summer and the dominant wavelengths and purities observed in the fall. The upper line records the 1986 values while the lower line records the 1987 results at each station.

Also included within Table 2 are turbidity values for each river station. Turbidity values were not obtained with the October 1986 optical data set. However, data from the regular Water Quality Branch Survey are listed in Table 2 when the Survey samples were obtained within a 24 hour period of the October 1986 spectro-optical measurements.

Dominant Wavelengths and River Basin Types

Glacier dynamics has accounted for much of the temporal evolution of the British Columbia land-forms which display ubiquitous consequences of glacial ice erosion and deposition. Of the fourteen stations studied in the current work, eight are more responsive to glacial melt intrusions (the 3 Columbia River stations, the 3 Kootenay River stations, and the Bull and Elk River stations) than are the others. That is, stations 5, 6, 7, 8, 9, 10, 11 and 12 may contain significant consequences of a temporally varying glacial melt component, while stations 1, 2, 3 and 4 display minimal consequences of glacial melt intrusions. Stations 13 and 14 are far removed from the direct impact of glacial melt but glacial activity takes place within the drainage basin of these two rivers. In the ensuing discussions we will refer to stations 5-12 as glacier-fed and the remaining stations as non glacier-fed despite the realization that such a distinction is somewhat arbitrary.

The river water compositions are considered to be represented by the process hydrographs given

TABLE 2. Dominant wavelength, spectral purity, and measured turbidity for British Columbia river stations.

Station Number	River and Location	Dominant Wavelength Summer (nm)	Purity (%)	Summer Turbidity (JTU)	Dominant Wavelength Fall (nm)	Purity (%)	Fall Turbidity (JTU)
1	Similkameen River at U.S. Boundary	575	46	3.4	567	47	—
		569	43	0.8	549*	22	0.1
2	Okanagan River at Oliver	563	28	1.0	573*	46	0.2
		575*	46	0.5	578*	59	0.4
3	Kettle River at Midway	578	26	1.5	582	59	2.6
		580	63	0.3	578	57	0.1
4	Kettle River at Gilpin	576	53	1.4	575	57	0.5
		573	53	0.5	571	55	0.3
5	Columbia River at Donald	—	—	—	571	36	—
		575	37	1.5	569	22	0.3
6	Columbia River at Revelstoke	—	—	—	540	17	—
		562	31	8.9	553	26	1.0
7	Columbia River at Trail	567	16	1.5	—	—	—
		574	17	0.5	570	20	0.3
8	Kootenay River at Canal Flats	—	—	—	512	8	—
		558	13	13.0	489	20	0.2
9	Kootenay River at Fenwick Station	581	46	77.0	570	31	—
		573	31	16.0	551	15	0.3
10	Kootenay River at Creston	571	46	1.2	556	42	2.4
		570	46	0.8	554	27	0.3
11	Bull River at Hatchery	562	20	4.7	555	21	—
		552	12	1.4	507	13	0.1
12	Elk River at Highway #93	572	21	125.0	574	37	—
		572	29	0.5	548	10	0.1
13	Thompson River at Spences Bridge	—	—	—	572	47	1.9
		568	42	2.2	573	49	0.3
14	Fraser River at Hope	576	28	43.0	579	61	10.0
		574	17	32.0	575	44	1.6

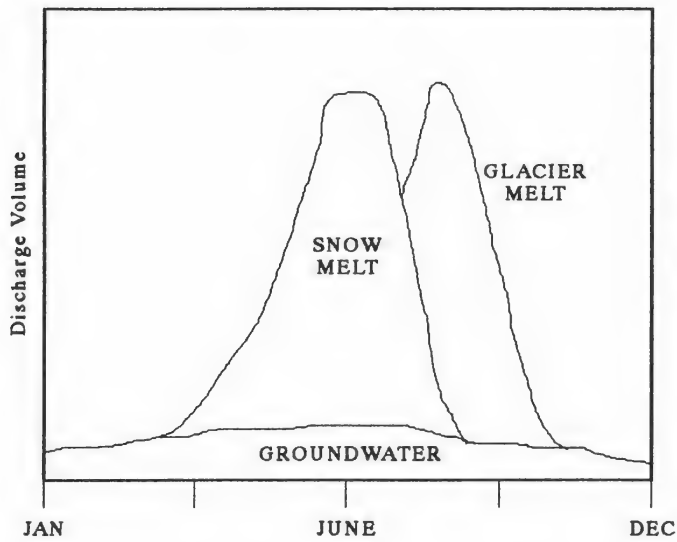
* contains interference from bottom reflectance

in Figure 5. Herein are sketched the anticipated seasonal dependencies of a representative river station which is glacier-fed and one which is non glacier-fed. The relative roles of snowmelt, glacial melt, and groundwater are illustrated in Figure 5. The role of groundwater for stations responsive to both snowmelt and glacial melt is distinctly less significant than the role of groundwater for stations only minimally impacted by glacial feed. While snowmelt and glacial melt are undoubtedly defined by suspended particulates displaying physical and optical differences, the composition of both types of runoff is almost exclusively inorganic in nature. The composition of groundwater, however, has a high probability of containing a substantial dissolved organic component in addition to its inorganic component. Consequently, non glacier-fed

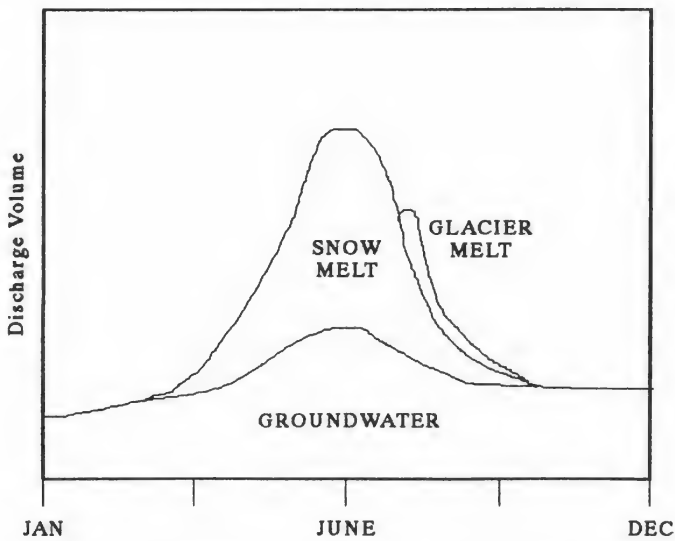
stations have a stronger likelihood of displaying the optical effects of a dissolved organic component than do glacier-fed stations.

Hence, summer optical spectra may be considered to represent river water comprised predominantly of snowmelt at glacier-fed stations, and some combination of snowmelt and groundwater at non glacier-fed stations. That is, summer subsurface volume reflectance spectra represent an optical response to suspended inorganic material at glacier-fed stations and an optical response to an admixture of organic and inorganic materials at non glacier-fed stations.

The fall optical spectra measured at glacier-fed stations may be considered to represent river water comprised of glacial melt containing suspended inorganic material. At non glacier-fed stations the



GLACIER-FED RIVER STATIONS



NON GLACIER-FED RIVER STATIONS

Figure 5. Idealized hydrographs illustrating the relative roles of snowmelt, glacial melt, and groundwater as components of the discharge volume for a) glacier-fed river stations and b) non glacier-fed river stations.

fall optical spectra may be considered to represent river water comprised predominantly of ground-water containing some combination of organic and inorganic material.

The river station hydrographs of Figure 5 represent the ideal situations of a simplified one-stream basin of uniform elevation. Most river basins do

not display such a simplistic single source hydrographic profile. The dendritic patterns defining many river basins necessitate the integration of inputs from several possibly non-identical sources to obtain the realistic hydrograph for each river station. Figure 6 schematically illustrates a river basin that would require integration of a multitude of sources.

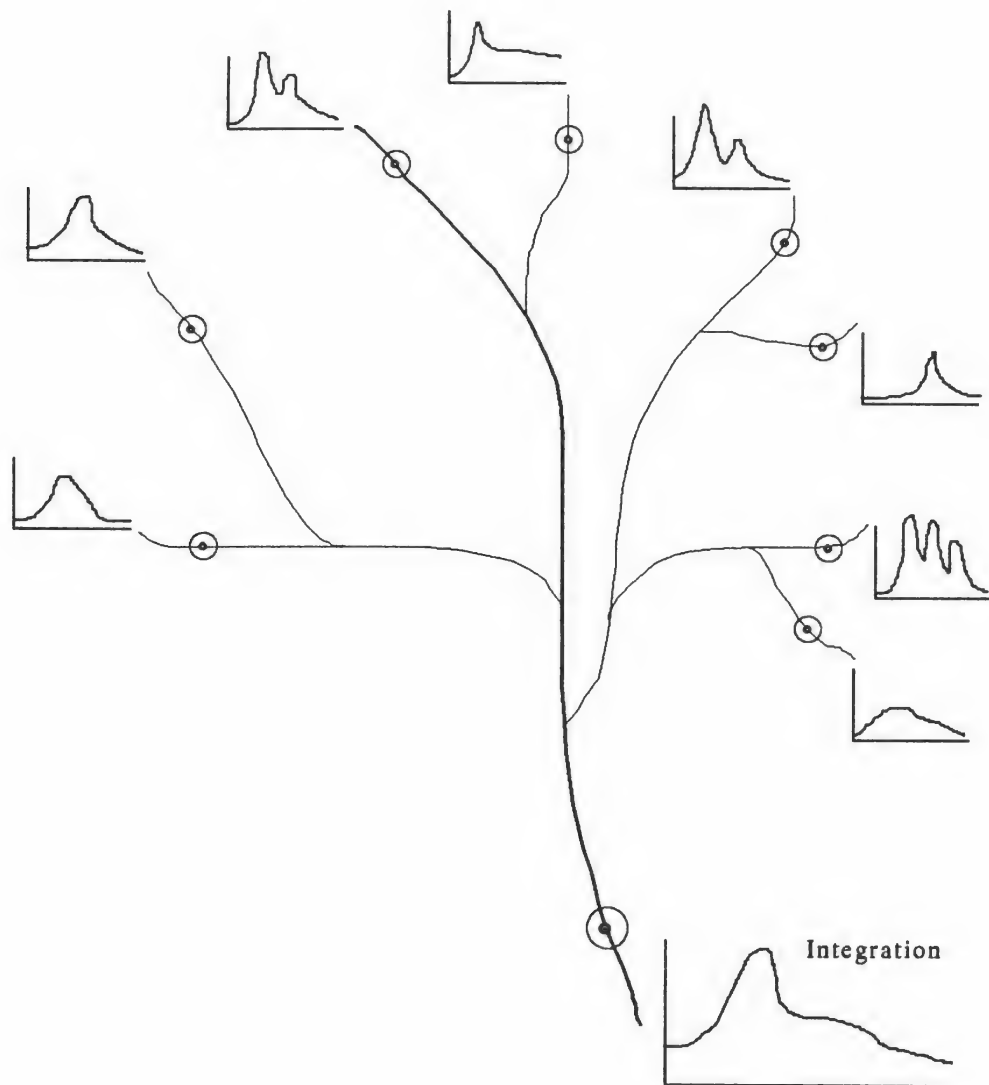


Figure 6. Schematic representation of a river station requiring the integration of hydrographs from multiple sources.

The Canadian Cordillera, like most large basin regions, therefore, can be considered as being comprised of a number of sub-units which can logically be divided into three basic types:

- Type 1: Simple sub-basins which are predominantly glacier-fed.
- Type 2: Simple sub-basins which are predominantly non glacier-fed.
- Type 3: Complex basins which are integrations of a multitude of Type 1 and Type 2 sub-basins.

The salient features of the data contained in Table 2 may be summarized as follows:

1. Most of the dominant wavelengths lie in the spectral range 555 nm to 585 nm. Lower spectral ranges (489 nm to 548 nm) of dominant wavelengths were recorded during fall visitations to stations 1, 6, 8, 9, 10, 11 and 12. The low value of dominant wavelength observed at station 1 (Similkameen River) is a consequence of bottom reflection. The other stations, however, are glacier-fed and belong to the Type 1 basin classification. Only two glacier-fed stations (station 5 Columbia at Donald, and station 7 Columbia at Trail) displayed no dominant wavelengths in this lower spectral range for either fall visitation. These two stations, however, qualify as belonging to the Type 3 complex basin classification due to the many tributaries of the Columbia River.
2. Quite substantial variations (13 nm-52 nm) were observed between the two fall determinations at all but one of the river stations influenced by glacial melt. Once again the Columbia River at Donald (belonging to the Type 3 basin classification) behaved differently from its glacier-fed counterparts, displaying a fall-to-fall variation of only 6 nm. Unfortunately, logistical difficulties prevented obtaining a reliable optical spectrum at station 7 in the fall of 1986.
3. In addition to the fall-to-fall variabilities observed in the dominant wavelengths for nearly all the glacier-fed river stations, these glacier-fed stations also generally displayed significant summer-to-fall wavelength variabilities (9 nm-69 nm). Again, as explained earlier, exceptions to this behaviour pattern are the Columbia River stations at Donald and Trail.
4. Little variation (≤ 10 nm) was seen between the two summer determinations at all the river stations when bottom effects are neglected.

5. For each non glacier-fed river station the summer and fall dominant wavelengths were numerically similar, displaying differences < 10 nm.
6. Wide ranges of turbidity were recorded throughout both sets of optical surveys. From Table 2 it is seen that low values of dominant wavelengths are always associated with low values of turbidity. High values of dominant wavelengths, however, can be associated with either high or low values of turbidity.

The features of the subsurface optical spectra observed in this study are not inconsistent with the theoretical results of our companion paper (Jerome *et al.* 1994) in which the dominant wavelengths of the upwelling irradiance spectra were related, through the optical cross sections of suspended minerals, chlorophyll, and dissolved organic carbon, to the co-existing concentrations of those aquatic components. Specifically:

1. Waters displaying low turbidity (i.e. low concentrations of suspended mineral and chlorophyll) along with low concentrations of dissolved organic carbon would be expected for glacier-fed, runoff-dominated river stations. These stations would display upwelling irradiance spectra characterized by low values of dominant wavelength.
2. Waters displaying low turbidity coupled with substantial concentrations of dissolved organic material would be expected for non glacier-fed groundwater-dominated river stations. These stations would display upwelling irradiance spectra characterized by intermediate to high values of dominant wavelength.
3. Waters displaying high turbidity could be expected for any station be it glacier-fed, non glacier-fed, or a complex integration of several Type 1 and/or Type 2 sub-basins. Such stations would display upwelling irradiance spectra characterized by high values of dominant wavelength.

Dominant Wavelengths and Basin Parameters

Since the dominant wavelength observed at a river station is a direct consequence of the organic and inorganic matter comprising the water column at the time of observation, the dominant wavelength can logically be expected to be dependent upon

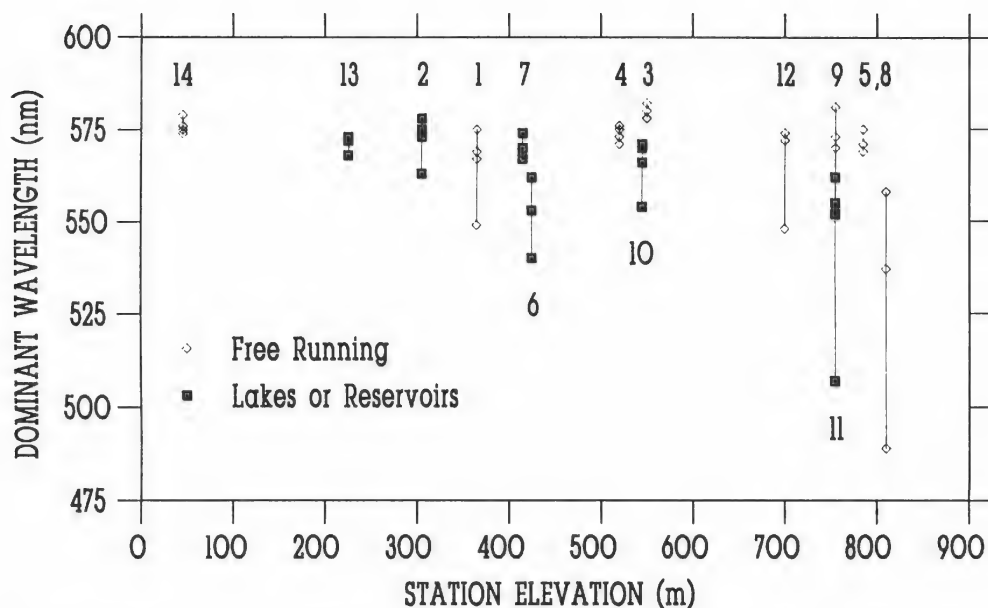


Figure 7. Range of dominant wavelengths observed at each river station plotted against the station elevation. Stations are numbered as in Table 1.

those basin parameters and/or activities that dictate aquatic composition. In addition to the nature and source of the water, such basin parameters as elevation, discharge flow rates, drainage area, and the presence and size of reservoirs and lakes can influence the quantities of the organic and inorganic components in river waters. Possible relationships among British Columbia river water colour and these basin parameters were explored.

Figure 7 displays the range of dominant wavelengths (summer and fall of each of two years) plotted against the station elevation in metres. Stations in rivers containing lakes or reservoirs are distinguished in Figure 7 from those stations in rivers that are free running. The presence of lakes or reservoirs can modulate river flow which may or may not result in a colour differential being observed between river water entering and vacating the lake or reservoir.

Figure 7 suggests a relationship between range of dominant wavelength and station elevation with stations at higher elevations displaying a wider range of dominant wavelengths. For the stations included within this study, the presence or absence of impoundments in the river does not appear to significantly impact this relationship. The stations

showing the highest elevations, and therefore the largest wavelength range in Figure 7 are the glacier-fed stations. Further, as seen from Figure 7, the upper limit to the range of dominant wavelengths appears to be independent of the elevation of the station sampled. Consequently, it is the lower limit of the dominant wavelength range which is inversely related to station elevation. As discussed in our companion paper (Jerome *et al.*, 1994), low values of dominant wavelength are associated with aquatic regimes containing small concentrations of suspended inorganic material. This suggests that glacial meltwater is characterized by either low turbidity values (if the optical cross sections of suspended mineral in the B.C. rivers are comparable to those observed for suspended minerals in Lake Ontario) or possible intermediate turbidity values (if the suspended mineral in the glacial meltwater are characterized by a flat, i.e. "white" optical cross section spectrum). In either case, the direct observations of this experimental work appear to be in good agreement with the theoretical analyses of our companion work.

There is evidence to support the possibility that a "white" optical cross section spectrum may indeed define the suspended material in the glacial

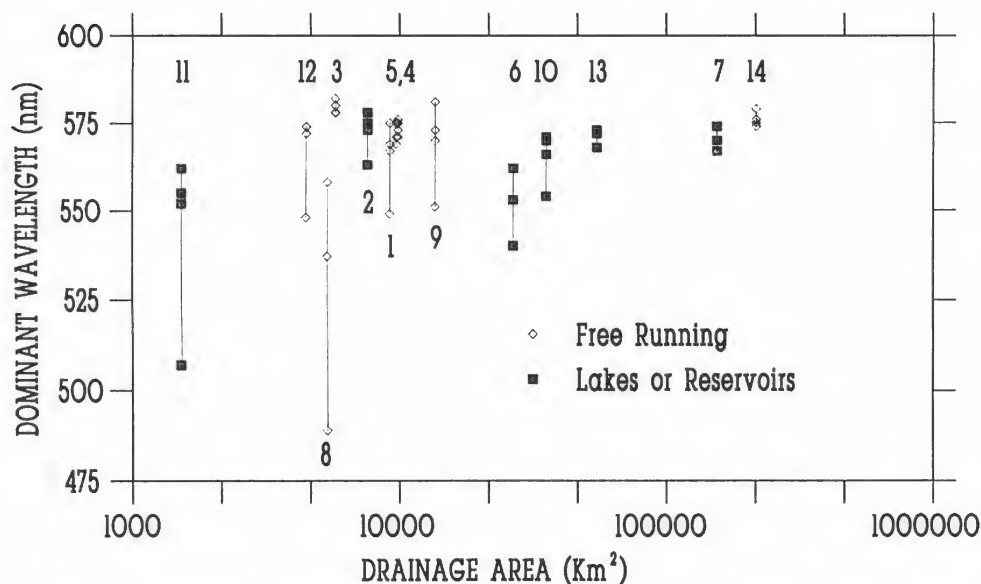


Figure 8. Range of dominant wavelengths observed at each river station plotted against the drainage area of the river upstream from the station. Stations are numbered as in Table 1.

feed. Low values of the chromaticity purity (as seen from Table 2) are generally observed for glacier-fed stations. Also, the very high values of volume reflectance observed in the glacier-fed stations Canal Flats and the Hatchery are strongly suggestive of the presence of "white" scattering centres. These B.C. river observations are consistent with the work of Aas and Bogen (1988) who observe that the "milky" runoff of some Norwegian glaciers is a consequence of larger diameter particles which tend to settle out downstream. Such settling could certainly be hastened by the presence of impoundments within the river, although free running rivers could also be characterized by such settling, depending upon stream flow velocity.

Figure 8 displays the range of dominant wavelengths plotted against the drainage area of the river upstream of the station location. A general relationship appears to emerge, with stations associated with large drainage areas displaying a relatively constant value of dominant wavelength, and stations associated with smaller drainage areas displaying larger ranges of dominant wavelength. This is undoubtedly a consequence of large drainage areas being associated with river stations belonging to the complex Type 3 classification. Such integrated source stations would tend to be

characterized by waters displaying high degrees of homogeneity. Once again the presence or absence of impoundments appears to be of little or no significance.

No distinct relationship between range of dominant wavelength and mean annual flow emerged for the stations considered in this study.

Conclusions

For the Canadian Cordillera, Type 1 sub-basins may be defined as having the following properties: high elevation, small drainage areas, strong influence from runoff associated with both snowmelt and glacial melt, low to moderate turbidity values, relatively constant upper limit of dominant wavelength, and non constant lower limit of dominant wavelength. These Type 1 sub-basins generally display dominant wavelengths in the wavelength interval 480-550 nm., i.e. colours perceived to be in the range blue to turquoise to green, a consequence of predominantly suspended inorganic materials.

Type 2 sub-basins may be defined as having the following properties: lower elevations, large or small drainage areas, minimal influence from glacial meltwater, substantial influence from snowmelt

and from groundwater intrusion, low to high turbidity values, and relatively constant upper and lower limits of dominant wavelength. These Type 2 sub-basins display dominant wavelengths in the wavelength interval 550-570 nm., i.e. colours perceived to be in the range green to brown, a consequence of substantial concentrations of dissolved organic materials.

Type 3 basins may be defined by any combination of the physical basin parameters (elevation, drainage area, source waters) defining the Types 1 and 2 sub-basins. Dominant wavelengths in the wavelength interval 573-578 nm were consistent features of the optical spectra observed at these stations. This suggests that the Cordilleran waters

tend to approach an "end-point" aquatic colour defined by dominant wavelengths of these values. This is consistent with the "end-point" dominant wavelength values 572-583 nm illustrated in our companion paper (even though the optical cross sections appropriate to Lake Ontario were used in generating those results). Such "end-point" aquatic colour with the 573-578 nm dominant wavelength range could be attained in any of three possible ways: 1) high concentrations of suspended minerals, 2) high concentrations of chlorophyll, or 3) low concentrations of suspended minerals coupled with high concentrations of dissolved organic materials. River water at stations included within Type 3 basins consistently display brown colours.

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Book Review

Two Views of Ecological Issues in Forestry

Reviewers:

Ken Lertzman, Bryan Evans, and Brenda Morehouse, School of Resource and Environmental Management, Simon Fraser University, Burnaby, B.C., Canada V5A 1S6

Helen Davis, and Therese Poland, Department of Biological Sciences, Simon Fraser University, Burnaby, B.C., Canada V5A 1S6

Balancing Act: Environmental Issues in Forestry. Hamish Kimmins. 1992. U.B.C. Press, Vancouver. 244 p. \$29.95. ISBN 0-7748-0435-1.

Seeing the Forest Among the Trees: The Case for Wholistic Forest Use. Herb Hammond. 1991. Polestar Book Publishers, Vancouver, B.C. 309 p. \$46.95. ISBN 0-919591-58-2.

What is an old-growth forest? How do forestry practices such as clearcutting and slash burning affect forests? How can we sustain forests and maintain an economically-viable forest industry? These questions are at the forefront of the often heated controversy over forestry practices and land use in British Columbia and the American Pacific Northwest. The two books reviewed here, though very different in orientation and scope, both contribute usefully to the debate.

Hamish Kimmins is a forest ecologist and Professor in the Department of Forest Science at the University of British Columbia. His book, *Balancing Act* provides an introduction to the application of ecological principles to the science of forestry. Herb Hammond is a Registered Professional Forester in British Columbia, a forest ecologist and citizen activist. His book, *Seeing the Forest Among the Trees* explores problems with current forestry practices and calls for a comprehensive reevaluation of how forests are managed and how benefits are distributed within society. Both books are intended for a general audience and assume no technical expertise in forest ecology or management. The contrasting views these authors present will also be valuable for professionals and academics interested in the public debate on forestry and forestry's role in society.

Kimmins' goal for *Balancing Act* is to provide an unbiased, scientific introduction to ecological aspects of forestry. He focuses on the stand-level

ecological consequences of tree crop production. Though he has many examples from the forests of northwestern North America, he also draws material from a variety of other forests around the world. The first third of the book introduces basic ecological principles of forest management, and the remaining two-thirds deal with a number of contentious issues. Kimmins begins by contrasting the time-scale of human perception with the inherently longer time-scale of change in forests. This is followed by a discussion of the major characteristics of forest ecosystems, the basics of production ecology, nutrient cycling in forests, and the processes of successional change. He concludes this part of the book with an introduction to the concept of ecological rotations which leads into the next chapter on forest management. Kimmins' "brief primer on forestry" is an excellent introduction to basic concepts of forest and stand management, including silvicultural systems, annual allowable cuts, and sustained yield.

In the following chapters, Kimmins explores such current issues as management practices, old growth and biodiversity, and the impacts of global change on forestry. The management practices discussed are limited to the ecological impacts of clearcutting, slashburning, and the use of herbicides and insecticides. Kimmins contrasts situations in which these management practices are and are not appropriate. He successfully conveys the inherent complexity of forest ecosystems and emphasizes that the appropriateness of management prescriptions depends on local ecological conditions. He concludes that such traditional practices as clearcutting, if used carefully, can be useful and appropriate tools for the manager.

This book is strongest in areas where Kimmins has substantial research background—nutrient cycling and the consequences of various management practices in terms of their effects on tree growth and site productivity. In other areas, notably

those relating to conservation issues, Kimmins' arguments are weaker and his conclusions sometimes surprising. In these cases, the paucity of directly cited sources is disappointing. Kimmins seems to believe that conservation concerns are primarily value driven, in contrast to timber management. This tends to downplay legitimate scientific concern for the loss of biological diversity. For instance, Kimmins claims that recent moratoria on timber harvesting in temperate forests are a result of environmentalists misapplying concerns about species loss associated with forest harvesting in the tropics (p. 150). He uses the controversy over the Northern Spotted Owl as an example of this. We were disturbed by this apparent dismissal of the substantial scientific effort supporting concerns about forest management and biodiversity. Pielou (1993) provides a detailed critique of Kimmins' approach to biological diversity.

Overall, *Balancing Act* delivers a good introduction to forest ecology and forest practices, providing a well-rounded description of the goals, methods and perspectives of modern forest management. Unfortunately, the book fails to achieve Kimmins' stated goal of scientific objectivity. He detracts from his otherwise excellent presentation by adopting a patronizing view of environmentalists and environmental concerns that is neither helpful nor, in our experience, entirely accurate.

In *Seeing the Forest Among the Trees*, Hammond offers a wide ranging discussion of many aspects of forests such as ecology, economics, politics, and spiritual values. The book is a personal statement, reflecting Hammond's love and knowledge of the forest and his disillusionment with current forestry practices. He acknowledges at the outset that he is a forest advocate and encourages the philosophy of connecting "your heart to your head" as a method of developing an ecologically sound and compassionate relationship with forests. Hammond focuses on the forests and the systems of forest management in British Columbia, but believes his message to be general.

Throughout the book, Hammond builds toward a blueprint for "wholistic" forest use. He begins with an overview of forest ecology, emphasizing functional and structural diversity and the connectivity within and among ecosystems. The middle two-thirds of the book detail Hammond's views on key problems with forestry in British Columbia, from examinations of the institutional structure determining the use of forests to detailed discussions of the

impacts of forestry practices on water, wildlife and soils. These provide a useful discussion of how political and economic forces can contribute to problems related to sustainability, both ecological and economic. Hammond illustrates this with a litany of failures, abuses and unintended consequences of policies and practices that at times can be overwhelming.

Hammond's book is an excellent introduction to forestry planning issues in British Columbia and a good introduction to forest ecology. It differs from Kimmins in that the discussion of forest ecosystems is clearly embedded within a sociological and political context. Hammond considers the distinctions between who controls forests, who benefits by forest use, who pays for the impacts of forest use, and who is accountable for impacts of forestry practices. In attempting to go beyond just presenting a critique of contemporary forest management, he proposes a system of what he considers to be "wholistic forest use". Hammond's solution calls for fundamental reform of the tenure system to establish control by consensus-oriented community forest boards. He outlines a model for land zoning for cultural values, ecologically sensitive areas, fish and wildlife, recreation/wilderness, and "wholistic" timber management.

A key component of Hammond's "wholistic" forest use is the potential to be gained from value-added manufacturing. For instance, he claims that as much as ten times the employment per unit of wood could be obtained by value-added manufacturing and labor intensive harvesting techniques. Unfortunately, the data to support this claim are lacking. Although value-added and labor-added approaches to forestry are widely touted as some of the best opportunities to stem forest industry job loss, the details of how this might be made a reality remain uncertain.

Hammond clearly has a passion for his subject and a vision for the kind of future he would like to see. The book's overall strengths and weaknesses both flow directly from these factors: those who want a dispassionate analysis or have a very different vision for forestry and forest dependent communities will find much to disagree with. Hammond's strength is his ability to integrate the ecological, social and institutional issues into a coherent framework. Whether or not his proposals for "wholistic forest management" can be made into reality, and whether they will in fact achieve his ecological and social goals remains to be tested.

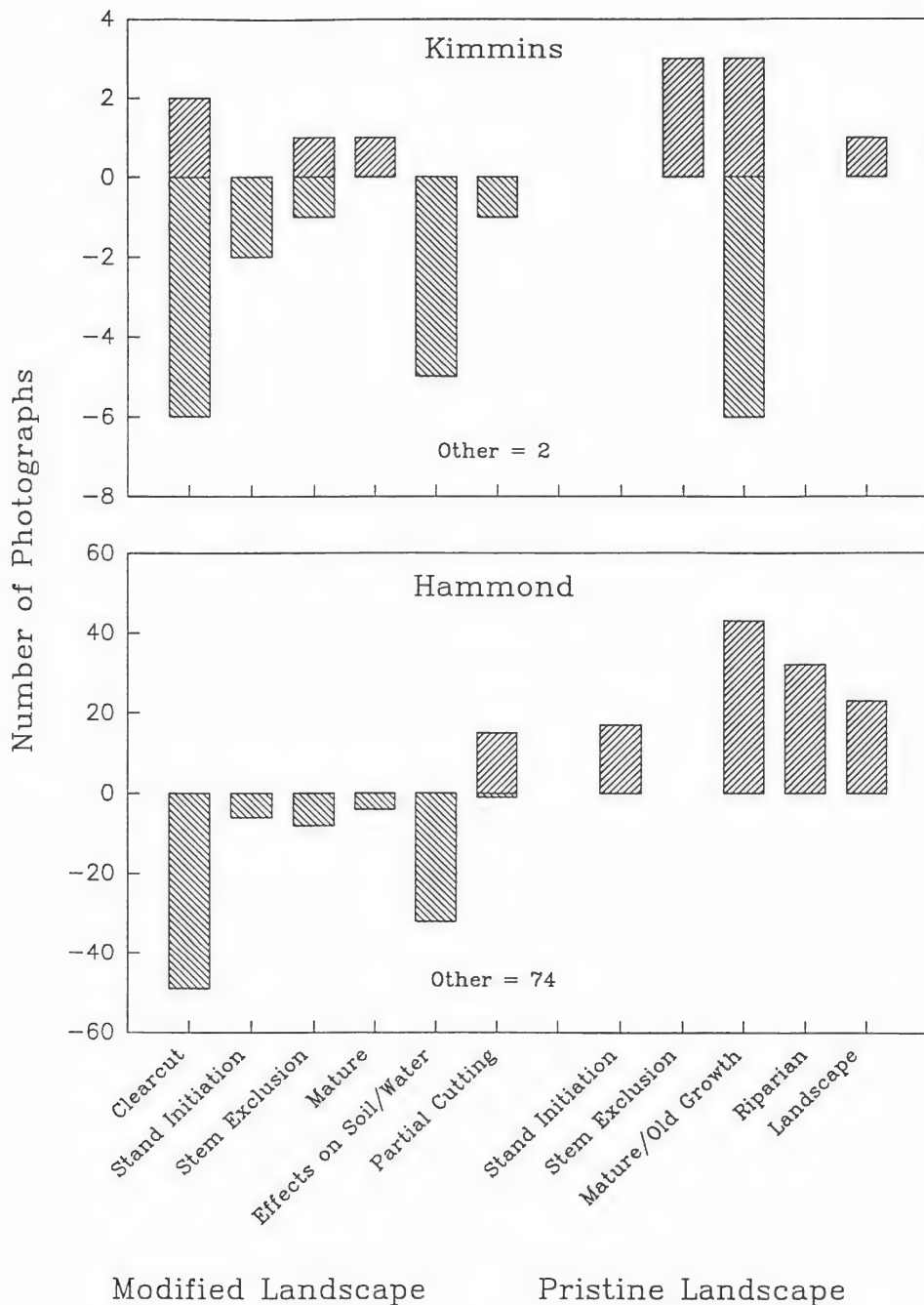


Figure 1. Number of photographs of modified and pristine landscapes in various conditions depicted by Kimmins and Hammond. The sign of the bar reflects the values (positive or negative) the author intended to illustrate with the photograph or caption.

In the first chapter of *Balancing Act*, Kimmins criticizes the misuse of photographs which freeze in time the dynamics of forest ecosystems. Both Kimmins and Hammond use photographs to illustrate their points. The cover of *Balancing Act* shows a stand of lush, managed, second growth in which the field of view is filled with trees. The cover photograph of *Seeing the Forest Among The Trees* shows logs, soil, small shrubs and herbs, and a conifer seedling. To examine how the different philosophies of each author might be reflected in photographs they used, we counted the number of photographs in each book in several stages of forest development and classed them as to whether they were of managed or wild subjects and whether they appeared to portray their subject as negative or positive. There was necessarily some subjectivity to our classification.

Hammond uses 304 photographs in his book to support his arguments for wholistic forest use. There is a distinctly unequal distribution of photographs, whereby modified landscapes are presented in a negative light and pristine landscapes in a positive light (Figure 1). Kimmins presents only 34 photographs. Photographs in *Balancing Act* cover fewer stages of forest development than in *Seeing the Forest Among The Trees* and the portrayal of positive and negative photographs is more equally distributed among modified and pristine landscapes (Figure 1). Oddly enough, in *Balancing Act*, twice as many photographs are used to illustrate negative points as show positive aspects of forests and forestry.

Kimmins claims to be objective in his assessments, whereas Hammond states *a priori* his sub-

jectivity. Despite this, both books reflect the ideologies of their authors. While they share a common goal of educating the public towards achieving sustainable forestry, each writer casts the issues in terms of his own biases. Whereas Kimmins focuses almost exclusively on ecological issues, Hammond spends relatively little time on strictly ecological issues but pursues the social, administrative and economic context in which the ecological issues are embedded. While Kimmins clearly recognizes that status quo forestry practices can have negative ecological consequences when misapplied, his general message about forestry as practiced today is positive. Hammond presents a gloomy picture about the same set of practices.

It is difficult to determine which author is closer to the truth. It seems to be a general characteristic of the forestry debate that each side points to specific instances of practices which support their perspective without presenting statistical evidence to support the notion that in fact the types of practices they highlight are prevalent on the landscape. We know of no recent material in the refereed literature which attempts a comprehensive evaluation of the standards of forestry which are in reality practiced in the Province. Unfortunately, recent government studies paint a picture closer to Hammond's than Kimmins' (Utzig and Walmsely 1988; Tripp et al. 1992; Tripp 1994). Whatever the recent history of forest practices, the host of new initiatives currently underway, such as the proposed Forest Practices Code (BC Ministry of Forests 1993a, b), promises hope for the future.

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1994 MEETING
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NORTHWEST SCIENCE



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Abstracts

Sixty-seventh Annual Meeting of the
Northwest Scientific Association
March 23-26, 1994

Central Washington University, Ellensburg, Washington

- 112 Abstracts
- 160 Author Index to Abstracts
- 163 Keyword Index to Abstracts

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The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

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David L. Peterson
Cooperative Park Studies Unit
College of Forest Resources
University of Washington, AR-10
Seattle, Washington 98195

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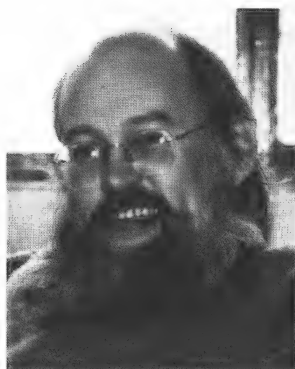
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Announcements

Dr. Fred L. Bunnell: Outstanding Scientist Award

Dr. Bunnell is arguably British Columbia's most respected and influential wildlife biologist. His scientific career epitomizes the criteria for the Outstanding Scientist Award, as Dr. Bunnell has devoted his life to studying, managing and enhancing Pacific Northwest ecosystems. He is an internationally-recognized scientist, and has authored 42 articles in refereed journals. He has also published an additional 46 papers in refereed government publications and proceedings, plus 21 review articles and books.



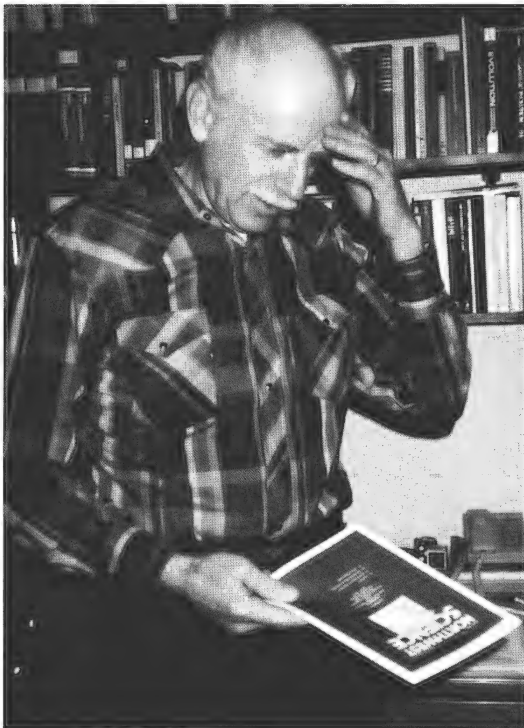
His reputation for fairness, and his skillful ability to integrate science with management, are valued commodities that are highly admired and appreciated by the international community. Over his career, he has presented 50 workshops and held consultancies in more than a dozen countries on topics dealing with integrated resource management. He was the only Canadian on a "blue ribbon" panel to review the Bureau of Land Management's long-term plans for Pacific Northwest forest lands.

Dr. Bunnell has also held several commissions with the Canadian government, most notably to review and implement the Beverley and Kaminuriak Craibou Herd Management Plan in the Northwest Territories. He also serves on the Committee on the Status of Endangered Wildlife in Canada.

Within the Pacific Northwest, Dr. Bunnell's expertise is in nearly constant demand. He is a member of the Vancouver Foundation, and has served on various Provincial committees dealing with Old Growth Strategy and Coastal Biodiversity Guidelines. He has recently been appointed by the Provincial Government to lead a team of independent scientists to propose and assess management guidelines that will alleviate land-use conflicts in Clayoquot Sound.

To better pursue his unwavering commitment to improved management based on scientific principles, Dr. Bunnell recently conceived, established and developed the Centre for Applied Conservation Biology at the University of British Columbia. The Centre has attracted some of British Columbia's most promising resource scientists. Based on this focused research collaboration, Dr. Bunnell's group has published 25 refereed articles, all of them dealing specifically with Northwest ecosystems.

The Northwest Scientific Association is pleased to honor and recognize Dr. Fred L. Bunnell as its Outstanding Scientist for 1994.



Honorary Life Member Award

Dr. Ronald J. Taylor was honored at the 67th Annual Meeting of the Northwest Scientific Association. He was presented with an Honorary Life Member Award for his service to the association as a former President (1978) and valued member of the Board of Trustees. Dr. Taylor joined the NSA in 1964 when he became a member of the biology faculty at Western Washington University. For the past 30 years he has been an active contributor to the business of the NSA, and he was the program chairman for the annual meetings held at WWU in 1979 and 1992. During this time he has contributed seven scientific articles to *Northwest Science*. He was the major advisor for fourteen graduate students working on their M.S. degrees. Dr. Taylor has had a direct and active role in conservation. He was a member of the Washington State Natural Heritage Advisory Council, member of the Washington Native Plant Society (Board of Directors and chairman of the research advisory committee), member of Washington

State Rare Plant Consortium, and the active mover in the preservation of the Lake Louise Ecological Site (near Bellingham, WA). He was also active in the successful effort to encourage the USDA Forest Service to set aside the Chowder Ridge subalpine site (north slope of Mt. Baker) as a research natural area. Dr. Taylor is an accomplished photographer and author, and has published several popular books on the identification and natural history of flowering plants in the Pacific Northwest. He is a long time member of the Northwest Scientific Association, and clearly worthy of this Honorary Life Member Award.

1994 Student Research Grants

Each year the Northwest Scientific Association conducts an annual student research proposal competition. Small monetary awards are provided to support student research projects at colleges throughout the Northwest. Funds for this activity come from member contributions to the Association's research fund.

As in past years, several excellent proposals were received for this year's competition, and six winners were announced at the 1994 meeting of the Northwest Scientific Association in Ellensburg, Washington. The winners and their research topics are as follows:

Debra Patla, Idaho State University—The effects of habitat modification on a spotted frog population in Yellowstone National Park (\$450)

Sherri Rodgers, Western Washington University—Defense mechanisms of the nudibranch feeding on sea pens in Puget Sound (\$450)

Michael Schumaker, Washington State University—The effects of UV-B radiation on ecophysiology of *Populus* species (\$400)

Jodi L. Johnson-Maynard, University of Idaho—Changes in andisol chemistry induced by successional plant communities in the grand fir mosaic ecosystem (\$300)

Ann Murkowski, Western Washington University—An investigation of *Macrocystis integrifolia-Nereocystis luetkeana* hybrids using DNA sequencing (\$200)

Ken Berger, University of Idaho—Calibration of tooth wear age categories in shrews with cementum annuli (\$200)

Summary of Minutes of the Board Meeting of the Northwest Scientific Association (Ellensburg, Washington; March 25, 1994)

1. Drafts of a proposed brochure targeted for use in soliciting support for NSA grants from private sector members were circulated and discussed. Board members Minore, Lavender, and Keller have been working on these brochures and will take comments into consideration in revising the text to produce a final draft that will be presented at the autumn 1994 Board meeting.
2. *Northwest Science* Editor Peterson reported that the backlog of manuscripts for the journal has been largely eliminated. Target turnaround for each stage of review and revision is eight weeks.
3. In the Treasurer's report, Dr. Hansen noted a reduction in interest income and that the balance of \$43,434 is about \$3000 less than for 1993.
4. Dr. Pitt, Chair of the Honors and Awards Committee, noted that nominations for the Outstanding Scientist and Honorary Life Member had been approved by the committee and would be announced at the business meeting.
5. Dr. Taylor, Chair of the Nominations Committee submitted the following for the coming year: President—Barry Keller, Idaho State University; President-Elect—Jan Henderson, USDA Forest Service; Treasurer—David Hansen, Pacific Lutheran University; Secretary—Denis Lavender, retired, Corvallis, Oregon.
6. Dr. Wright, Chair of the Student Awards Committee, reported that the committee received 15 proposals and had recommended funding six of them for total funding of \$2000.
7. Dr. Keller indicated that the annual NSA meeting scheduled for Idaho State University, Pocatello, Idaho in 1995 will probably be held during the third week of March. He expects that the Idaho Chapter of the Wildlife Society will meet with the NSA.
8. The annual NSA meeting for 1996 is scheduled for the third week in March at Pacific Lutheran University, Tacoma, Washington. The annual NSA meeting for 1997 is scheduled for the third week in March at Eastern Washington University, Cheney, Washington.

Using General Land Office Records to Assess Forest Succession in Ponderosa Pine/Douglas-fir Forests in Western Montana

Abstract

Original (1901 and earlier) General Land Office (GLO) records were used to quantify successional changes in Ponderosa Pine/Douglas-fir (*Pinus ponderosa* / *Pseudotsuga menziesii*) forests in western Montana following altered fire regimes. GLO bearing tree data provided the means to reconstruct presettlement forest structure in the study area: the former Fort Missoula Timber Reserve (FMTR), located in Pattee Canyon near Missoula, Montana. Tree importance values, tree density values and basal area values were estimated from the GLO survey notes and compared to forest data collected in 1992 to assess successional trends. The results show that with reduced fire influence, Douglas-fir in FMTR has made major gains in stand dominance over ponderosa pine and western larch (*Larix occidentalis*), especially on north aspects; on south aspects, former savanna and grassland communities have experienced conifer invasions.

Introduction

Gaining an understanding of long term vegetation history and successional changes linked to human land use practices has become of increasing importance (Habeck 1990, Monnig and Byler 1992, Kaufmann *et al.* 1992). In western North America, for example, wildfire served as an important process in shaping pre-1900 vegetation patterns on Rocky Mountain landscapes. Post-1900 alteration of presettlement fire regimes, as well as logging, domestic grazing, mining, and land cultivation triggered significant changes in the vegetation structure and composition of this region. Some ecologists have linked modern changes in forest structure and composition to potential for severe fires, as well as to reduced forest health (Mutch *et al.* 1993).

In western Montana, Euroamerican settlement intensified and expanded in the 1870's. Prior to 1900 frequent, low intensity fires in the Douglas-fir zone, originating from lightning or from native American ignitions (Arno 1980, Gruell 1985, Barrett and Arno 1982), maintained ponderosa pine-western larch communities as open, park-like forests (Habeck 1990). This specific fire-vegetation relationship in western Montana was evident to early area witnesses (Ayres 1900, Leiberg 1899); circa-1900 photographs taken in western Montana often reveal grasslands and open ponderosa pine woodlands occupying much of the lower half of the area's mountain slopes (Leiberg 1899, Gruell 1983).

With the onset of a national policy of fire exclusion in the early 1900's, along with accelerated logging of old-growth forests, western Montana's montane pine-larch forests have experienced a rela-

tively rapid successional change toward Douglas-fir dominance (Arno *et al.* 1985, Habeck 1985, 1990). Pacific Northwest ecologists have been seeking more detailed, quantitative information on forest changes linked to human activity, including reduced fire (Kaufmann *et al.* 1992, Mutch *et al.* 1993). As resource managers consider how to make historically important processes, such as fire, a part of landscape management, they need to consider various forest structure and composition options. Towards these efforts, they are helped by having historic baseline data points to pre-1900 vegetation structure serving as references; GLO survey records provide such an opportunity (Noss 1985).

General Land Office Survey Records

Relatively detailed, quantitative descriptions of presettlement forest structure and composition can be derived from interpretations of General Land Office (GLO) survey records dating back, in western Montana, to the 1870-1910 era. The GLO notes, which provide data on bearing trees selected to document section corner locations, provide a means to reconstruct presettlement forests (Stearns 1949, Bourdo 1956, White 1976).

In practice, a section corner location was field-marked by a wooden stake or rock monument; the position of this corner was typically described by using four bearing trees, one in each of the four quadrants surrounding the corner. The bearing trees were to be "only the soundest and thriftiest of the trees, and of the size and kind which experience teaches will be the most permanent and lasting" (Stewart 1935). Also, the bearing trees selected were to be within 300 links (198 ft/60 m)

of the corner being described. Section corners located in savannas or grasslands, often did not have four trees near enough to serve as corner witnesses, and the notes reflected this in specific language, with only 1-3 trees recorded, or none. Tree species, tree diameter, tree distance from the corner, and compass bearing are recorded in the notes. The height at which diameters of bearing trees were to be taken was not specified in the guidelines.

It is necessary for ecologists to practice caution in extracting information from GLO survey notes. Surveyors contracted by GLO followed prescribed instructions in traversing survey lines and describing bearing trees; Stewart (1935) and Dodds (1944) provide details of the operational rules and regulations in effect circa 1900. In a particular locality, such as covered in this report, consideration must be given to the possible existence

of individual surveyor bias in applying or interpreting GLO guidelines, or the presence of errors in GLO notes for a specific township or section.

A surveyor might practice differential selectivity in bearing tree selection, partly based on the flexibility built into the guidelines for bearing tree selection, and partially on personal bias. White (1976), working in western Montana (Lubrecht School Forest, University of Montana), detected occasional surveyor bias against small-diameter trees as well as very large diameter trees in GLO notes covering his study area; the exclusion of very small and very large trees as witness trees seems to fit the guideline criteria for bearing tree permanency or longevity. In a preliminary stage of the present study, copies of the original GLO notes were taken into the field (upper Pattee Canyon, Figure 1) and matched with the trees on the modern landscape.

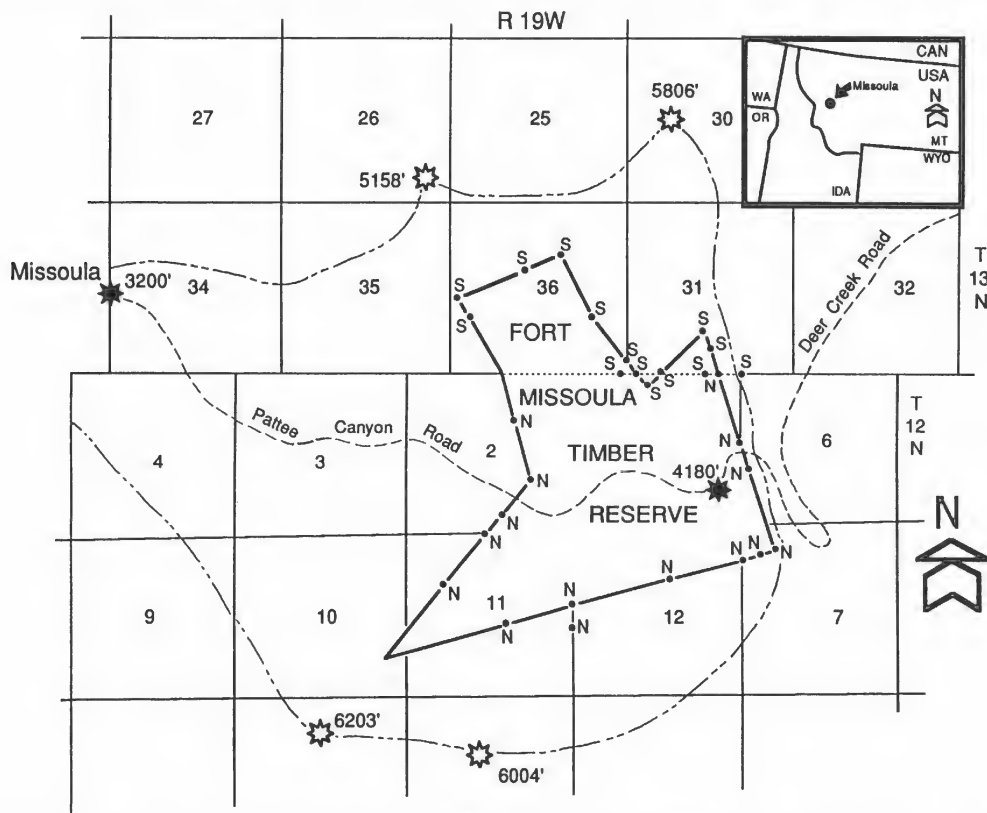


Figure 1. Locations of Pattee Canyon and the former Fort Missoula Timber Reserve (FMTR) in western Montana. The canyon's drainage boundary is shown in dot-dash line, and the canyon's main access road by a dashed line. Surveyed corners and FMTR boundary markers employed in this study are shown by letter symbols, "S" = south aspect sites ($n = 14$), and "N" for north aspect and ravine sites ($n = 15$).

Based on the presence and absence of living trees and the remains of earlier existing trees near revisited section corners, it was assessed that bias in surveyor witness tree selection was uncommon.

By revisiting the original section corners, and re-measuring existing trees at each survey corner, it is possible to estimate the direction of forest successional change. Such an effort was undertaken in a military wood and timber reservation, the former Fort Missoula Timber Reserve (FMTR), established in 1879 and located in Pattee Canyon (USDA Forest Service, Lolo National Forest) near Missoula, Montana (Lat. 46° 46' N, Long. 114° 50' W, Figure 1); the area is now called the Pattee Canyon Recreation Area (PCRA). Photo copies of the original GLO notes, dated 1901 or earlier, are available for Pattee Canyon and the FMTR in the Missoula County Surveyor's Office, Missoula, Montana.

History of Fort Missoula Timber Reserve

In 1879, a 648 ha (1600 acre) "wood reservation" was set aside by Executive Order in the upper reaches of Pattee Canyon (Figure 1) to fill the fuelwood and construction needs of Fort Missoula, a military facility located 8 km (5 miles) west of Pattee Canyon (USDA Forest Service 1991). The star-shaped boundary of FMTR (Figure 1) appears to have been laid out to encompass a specific concentration of large, (75-150 cm/ 30-60" in diameter) ponderosa pines and western larches occurring in upper Pattee Canyon.

Selection of Fort Missoula Timber Reserve

Fort Missoula Timber Reserve was selected to study historic forest changes for the following reasons: (a) the variety of forest and bunchgrass communities it supports is representative of the lower montane zone forest-grassland types commonly found elsewhere in western Montana; (b) the FMTR's irregular boundary, and its numerous intersections with township and section lines, provides an unusually high concentration of GLO survey corners ("sample points"), and thus an abundance of bearing tree data from relatively homogeneous landscape units; and (c) the relatively light logging disturbance in those portions of Pattee Canyon and FMTR where modern data needed to be taken. When FMTR's surveyed corners were revisited in 1992, only those that appeared to have

been the least altered by post-settlement disturbances (other than fire control) were included in the analysis.

Methods

Procedures used to extract phytosociologic information from GLO survey notes are well-documented (Cottam 1949, Bourdo 1956, Habeck 1961, Noss 1985, and Galatowitsch 1990). The General Land Office began contracting surveyors to subdivide public lands in western Montana in 1867, following field techniques standardized in the GLO's 1855 Manual of Instructions (Dodds 1944). GLO surveying parties created sets of field notes for the townships subdivided. Section corner locations were described using bearing trees. At the end of each surveyed mile, and after a township was subdivided, descriptions were provided that mention dominant tree species present, quality of timber, and assessment of agricultural potential. Sometimes the notes included information on general topography, soil quality and timber.

As section lines were being run, the surveyors made note of the line entering or leaving forest cover; the latter, in turn, might be further described as "heavily timbered," "heavy open timber" or "scattering timber." Based on my 1992 re-examination, the term "heavy," as used in the survey notes, is believed to have been used to characterize the presence of scattered "large-sized" trees, not necessarily "densely stocked" forests. Ascents and descents of slopes, intersections of gulches, ridges, roads, or fence lines were recorded, as were diameters and species of trees found directly on the line.

Bearing trees in quadrants surrounding the corners were chosen and described in the GLO notes. Typically, four bearing trees (the nearest one in each quadrant) were described at section corners (mile marks), while two trees were recorded at quarter-section (half mile) corners. An excerpt taken from the September 18, 1901 survey notes for the Third Mile along FMTR's boundary on Pattee Canyon's north aspect is as follows:

Chains

40.00

Set a sand stone 22 x 12 x 7 ins.,
16 ins. in the ground, for 2 1/2 Mile cor.
marked 2 1/2 M. on E.
T. R. on N. and
P. L. on S. faces; from which

A pine, 24 ins. in diam., bears N. 10° E., 38 lks.
dist.; marked Ft. M. T. R., 2 1/2 M., B. T.

A fir, 12 ins. diam., bears S. 60° E., 141 lks. dist., marked T. 12 N., R. 19 W., S. 12; 2 1/2 M., B. T.

A fir, 15 ins. diam., bears S. 45° W., 114 lks. dist., marked T. 12 N., R. 19 W., S. 12; 2 1/2 M., B. T.

A tamarack, 8 ins. in diam., bears N. 43° W., 67 lks. dist., marked Ft. M. T. R., 2 1/2 M., B. T.

The "40.00" represents a half-mile corner. The "pine" referred to is ponderosa pine, the "fir" is Douglas-fir, and the "tamarack" is western larch. The initials "lks" refers to links, one link equals 7.92". On FMTR's 1901 boundary re-survey, corners, mile marks and half-mile marks usually were described using four bearing trees. Also, wherever the FMTR boundary intersected township and section lines, the points were also described using four bearing trees, if available within the 300 link limit.

At the end of the surveyed "Third Mile", at 80.00 chains, the survey party chief provided the following summary, with the listing of trees in order of dominance, the most dominant listed first:

Land, broken N. slope of mountain.

Soil, sandy., 2nd rate.

Timber, pine, fir and tamarack.

Mountainous and heavily timbered land and through dense undergrowth 80.00 chns."

Bearing tree data resembles plot-less, point-centered distance measurement data (Cottam and Curtis 1956). GLO tree data, when summarized for a series of corners occurring on similar (relatively homogeneous) landscapes, allow calculation of importance values for each tree species defined as the sum of relative density, relative frequency and relative basal area. The distance measures also allow estimates to be made of tree densities (number per hectare) and basal areas (square meters per hectare) for all tree species recorded in the survey notes. Since a majority of the 1901 survey points were witnessed by four bearing trees, the average point-to-tree distances are directly related to tree mean area (MA), the value needed to calculate tree densities. In addition, it was assumed in using the 1901 GLO notes that sapling-sized trees, under 10 cm/4" in diameter at groundline, were not selected as bearing trees; no evidence was found in 1992 that trees over 10 cm/4", if alive, had been rejected as bearing trees. The 1901 notes provide data for 30 corner points and 82 bearing trees.

During 1992, the FMTR corners were revisited; one of the original corners could not be relocated (thus $n = 29$ for 1992). The presence and survivorship of the 1901 bearing trees at each corner point were noted. The diameters of surviving bearing trees were measured at 0.3 m (1 ft) above groundline, or "stump height." Random increment corings of surviving bearing trees at breast height (modern standard DBH, 1.4 m above the ground) and at 0.3 m (1 ft) confirm that diameters recorded in the 1901 notes do represent bearing tree diameters near their bases. White's study (1976) closely supports this finding. A larger sample of 324 presettlement bearing trees covering much of Pattee Canyon indicates that corner-to-bearing tree distances and compass bearings were precisely instrument-measured; bearing tree diameters were regularly recorded, but not exclusively, in even numbers such as: 10", 20", 30", or in multiples of a half-foot: 6", 12", 18", 24", suggesting surveyors simply estimated bearing tree diameters.

The 1992 data were taken at each corner revisited, employing the point-centered quadrant method (Cottam and Curtis 1956). The area around each corner point was divided into quarters using cardinal compass bearings, replicating the same set of quadrants used in 1901. The nearest tree in each quadrant over 10 cm (4") was recorded by species, diameter (30 cm (1 ft) above groundline) and distance (corner-to-tree). In addition, the nearest tree sapling (diameter 2.5-10 cm (1-4")), and nearest tree seedling (under 2.5 cm (1") diameter), but over 1 m (3 ft) high in each quadrant were tallied.

The 1992 data were used to calculate importance values (I.V.) for trees, saplings and seedlings for each species, as well as density and basal area per hectare for each tree species (Cottam and Curtis 1956). Within a 0.04 ha (0.1 acre) circular macroplot around each corner, estimated canopy coverage percentages (Daubenmire 1959) were assigned to each tree, shrub, and herbaceous species present. These latter data were employed in habitat typing (Pfister *et al.* 1977) each surveyed corner location.

To understand how presettlement forest vegetation in FMTR has changed over the past 90+ years, the survey corners were partitioned into two canyon subunits (Figure 1), each encompassing a set of survey corners occupying homogeneous canyon aspects. The FMTR corners occur on

TABLE 1. Post-settlement (1901-1992) forest change* on south aspects in Fort Missoula Timber Reserve, western Montana (Figure 1), based on GLO survey records.

A. 1901 South Aspect Forest Composition:									
Tree Species	Points Occur.	Number Trees	Basal Area	F %	Den %	Dom %	I.V. %	Density No./Ha	Basal Area/m ² /Ha
PIPO	12**	34	8.5	100	100	100	300	32.8	8.2
PSME	0	0	0.0	0	0	0	0	0.0	0.0
Totals	12	34	8.5	100	100	100	300	32.8	8.2
B. 1992 South Aspect Forest Composition:									
PIPO	14	53	7.5	88	95	99	282	125.2	17.7
PSME	2	3	0.1	12	5	1	18	7.2	0.2
Totals	16	56	7.6	100	100	100	300	132.4	17.9

* = Importance Values (I.V.) = summation of relative frequency (= F %), relative density (= Den %) and relative dominance (= Dom %) values. Density = trees per hectare, Basal Area = square meters per hectare. PIPO = *Pinus ponderosa*, PSME = *Pseudotsuga menziesii*.

** = In 1901, two surveyed corners in grasslands lacked nearby bearing trees. At other corners located in savannas, only 1-3 witness trees were recorded rather than the typical four. In 1992 four trees were recorded at each corner point.

TABLE 2. Summary of 1992 south aspect tree reproduction data* taken at original 1901 GLO survey corners in Fort Missoula Timber Reserve, western Montana.

A. South Aspect Tree Saplings:						
Species	Points Occur.	Number	F %	Den %	I.V. %	Density No./Ha
PIPO	12	35	57	63	120	66.4
PSME	9	21	43	37	80	40.0
Totals	21	56	100	100	200	106.4
B. South Aspect Tree Seedlings:						
PIPO	10	28	53	50	103	73.6
PSME	9	28	47	50	97	73.6
Totals	19	56	100	100	200	147.2

* = Importance Values (I.V.) = summation of relative frequency (= F %) and relative density (= Den %) values. Density = number of saplings or seedlings per hectare.

well-defined southern aspects, northern aspects, and several moist ravines; the latter two site categories were grouped for analysis.

Results

Corners occupying southern aspects fit conifer/grassland habitat types, including: ponderosa pine/bluebunch wheatgrass h.t. (*Pinus ponderosa*/*Agropyron spicatum* h.t.), ponderosa pine/Idaho fes-

cue h.t. (*P. ponderosa*/*Festuca idahoensis* h.t.), Douglas-fir/snowberry h.t. (*Pseudotsuga menziesii*/*Symphoricarpos albus* h.t.), and Douglas-fir/rough fescue h.t. (*P. menziesii*/*Festuca scabrella* h.t.). Stand data for south aspect survey corners are presented in Tables 1 and 2.

Survey corners on northern aspects are classified as Douglas-fir/ninebark h.t. (*Pseudotsuga menziesii*/*Physocarpus malvaceus* h.t.), with most fitting

TABLE 3. Post-settlement (1901-1992) forest change* on northern aspects of the Fort Missoula Timber Reserve, western Montana (Figure 1).

A. 1901 North Aspect Forest Composition:									
Tree Species	Points Occur.	Number Trees	Basal Area	F %	Den %	Dom %	I.V. %	Density No./Ha	Basal Area/ m ² /Ha
PIPO	14	25	5.2	47	52	72	171	24.7	5.1
PSME	9	11	0.7	30	23	9	62	10.8	0.7
LAOC	7	12	1.3	23	25	19	67	11.8	1.3
Totals	30	48	7.2	100	100	100	300	47.3	7.1
B. 1992 North Aspect Forest Composition:									
PIPO	6	7	1.1	21	12	19	52	40.5	6.5
PSME	14	36	2.8	50	60	45	155	202.5	15.4
LAOC	8	17	2.1	29	28	36	93	94.3	11.9
Totals	28	60	6.0	100	100	100	300	337.3	33.8

* = Importance Values (I.V.) = summation of relative frequency (= F %), relative density (= Den %) and relative dominance (= Dom %). Density = number of trees per hectare. Basal Area = values expressed in square meters per hectare. PIPO = *Pinus ponderosa*, PSME = *Pseudotsuga menziesii*, LAOC = *Larix occidentalis*.

TABLE 4. Summary of 1992 north aspect tree data* sampled at GLO survey corners in Fort Missoula Timber Reserve, western Montana.

A. North Aspect Tree Saplings:						
Species	Points Occur.	Number	F %	Den %	I.V. %	Density No./Ha
PIPO	6	13	23	20	43	30.1
PSME	12	27	48	50	98	74.8
LAOC	8	16	29	30	59	44.9
Totals	26	56	100	100	200	149.8
B. North Aspect Tree Seedlings:						
PIPO	4	7	20	13	33	24.2
PSME	14	46	70	82	152	153.6
LAOC	2	3	10	5	15	9.4
Totals	20	56	100	100	200	187.2

* = Importance Values (I.V.) = summation of relative frequency (= F %) and relative density (= Den %) values. Density = number of saplings or seedlings per hectare.

within the *Physocarpus malvaceus* phase. The latter phase includes cool, moist sites capable of supporting western larch. North aspect survey corners data are summarized in Tables 3 and 4.

South Aspects

Ponderosa pine was and continues to be the major overstory dominant on southern aspects. In 1901 (Table 1, Part A), the south aspect GLO corner notes recorded ponderosa pines exclusively as

bearing trees. The lower density of trees suitable as bearing trees on south aspects led, at times, to the surveyors recording only two or three bearing trees at corners where four trees would have been selected. In fact, two bunchgrass-dominated corner sites lacked, in 1901, bearing trees within the recommended 300 link distance, so none were recorded at these corners. The calculated 1901 south aspect tree density is 32.8 trees per ha (13.3/acre), suggesting an open-canopied pine

savanna prevailed; basal area averaged 8.2 m²/ha (36 ft²/acre). The 1901 ponderosa pine bearing trees averaged .25 m² (2.8 ft²) in basal area, and an average of 57 cm (22.8") in stump diameter.

At the south aspect points revisited (Table 1, Part B), the magnitude of forest change was very evident. Ponderosa pine still maintained its over-story dominance, but there has been a four-fold increase in tree density reaching 132.4 trees per ha (53.6/acre). In 1992 there was a greater density of pines, but those recorded averaged smaller diameters than those present in 1901, with basal areas averaging 0.14 m² (1.5 ft²), and diameters averaging 42 cm (16.8"). In 1992, three Douglas-firs were tallied at south aspect corners, indicating post-1900 entry of firs on warm, dry FMTR sites, perhaps capable of supporting forests classified within the Douglas-fir climax series (Pfister *et al.* 1977).

Sixteen (47%) of the original 34 south aspect bearing trees were alive in 1992, but these were not always recorded as the nearest tree(s) to the corners during the 1992 re-measurement. Bearing tree mortality appeared mostly due to natural causes (standing snags, wind-thrown logs, broken stumps), but a few of the original bearing trees, positioned on private property outside the FMTR boundary, appear to have been lost to logging, not withstanding the illegality of cutting and removal of section corner bearing trees. The basal areas of the 16 surviving ponderosa pines increased four fold, from an average of 0.11 m² (1.2 ft²), and 37.5 cm (15") in stump diameter in 1901, to 0.44 m² (4.8 ft²), and 75 cm (30") in stump diameter in 1992.

A summary of 1992 structure and composition of the sapling and seedling layers on south slope corners is given in Table 2. Comparable tree reproduction data are not available for 1901. Modern importance values (I.V.) for tree saplings show that Douglas-fir reproduction is currently well represented. Ponderosa pine saplings, originating over the past 3-4 decades, still outnumbered Douglas-fir saplings in 1992. Field observations indicate pine and Douglas-fir reproduction has been invading the open gaps between the old-growth ponderosa pines (Figure 2). The 1992 data show Douglas-fir seedlings equalling established ponderosa pine seedlings in density. Savanna-bunchgrass components are becoming reduced in total area without the frequent fire interventions on southern aspects. Succession towards the poten-

tial climatic climax stage dominated or codominated by Douglas-fir and/or ponderosa pine has progressed over the past ninety years (Pfister *et al.* 1977).



Figure 2. Entry of *Pseudotsuga menziesii* reproduction into an old-growth *Pinus ponderosa* community earlier maintained as a savanna by low intensity fires. Photo taken near eastern boundary of Fort Missoula Timber Reserve (Figure 1). Photo by J.R. Habeck, 1990.

North Aspects

The section corners occupying northern aspects and moist ravine sites in FMTR have western larch along with ponderosa pine and Douglas-fir as major forest components (Table 3); both western larch and ponderosa pine are fire-dependent and were favored by the frequent, low intensity burns occurring before 1900 (Habeck, 1990). Although western larch was present, the most common witness tree recorded at north aspect corners in 1901 was still ponderosa pine which displayed the highest importance value, the highest density and greatest basal area values (Table 3, Part A).

The 1992 data from north aspect and ravine corners (Table 3, Part B) show distinct shifts in

Fort Missoula Timber Reserve Pattee Canyon - Lolo National Forest Basal Area Data - North Aspect

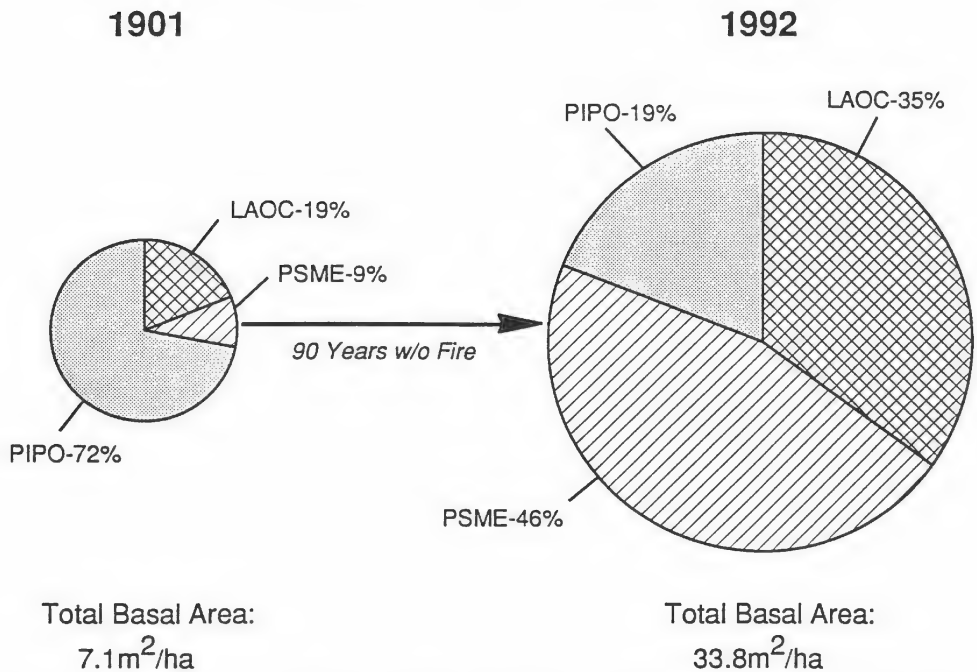


Figure 3. Ninety years of forest change in basal area (m²/ha) on north aspects in Fort Missoula Timber Reserve, western Montana. Percentages of total basal area per hectare are given for PIPO = *Pinus ponderosa*, PSME = *Pseudotsuga menziesii*, and LAOC = *Larix occidentalis*.

forest structure and composition towards Douglas-fir. Figure 3 emphasizes the significant increase in basal area per hectare, and the much greater importance of Douglas-fir on the modern FMTR landscape. All three conifer species have increased in density and basal area, changing the physical structure of forest cover from open to closed canopy; ponderosa pine has shifted, proportionately, to third place ranking within the modern FMTR forest. About 50% of the original 48 north aspect bearing trees survived to 1992, but these survivors, though larger in 1992 than in 1901, were scattered amongst thousands of smaller Douglas-firs established during the post-1900 era.

A summary of 1992 conifer reproduction data taken from FMTR's northern aspects is provided in Table 4. Although all three species remain pres-

ent in the lower forest stratum, Douglas-fir dominates the seedling and sapling layers, as might be expected of the potential climax species in the prolonged absence of fire. Ponderosa pine and western larch, although long-lived, benefit by site disturbances (mineral seed bed exposure) in their establishment. Eighty-two percent of all tree seedlings recorded during the 1992 sampling were Douglas-fir. As mature, old-growth ponderosa pine and western larch are lost through natural attrition, with limited replacement, the shift towards over-story dominance by Douglas-fir is predictable (Arno 1980, Habeck 1990).

Discussion

The successful use of GLO survey notes in the Fort Missoula Timber Reserve in assessing direction and

magnitude of post-settlement forest change is partly due to the uncommon concentration of surveyed corners in upper Pattee Canyon. The inclusion and description of bearing trees wherever the FMTR boundary intersected township and section lines expanded the quantitative database used to calculate circa-1900 forest structure and composition. Furthermore, the GLO survey note data for upper Pattee Canyon originate from relatively uniform south aspect and north aspect landscape units, allowing the grouping and averaging of the 1901 data. Elsewhere in mountainous parts of the Pacific Northwest, there may be difficulty in assembling a sufficient number of bearing trees to represent homogeneous landscapes supporting similar vegetation or closely related habitat types, as exist in Pattee Canyon. However, where similar analyses of GLO notes are undertaken, in areas lacking the spatial concentration of surveyed corners found in Pattee Canyon, it would be necessary to group bearing tree data taken from similar aspects and elevations within contiguous townships that share biophysical similarities.

Frequent presettlement fires in Pattee Canyon and elsewhere in western Montana are known to have generated and perpetuated pine-larch savanna and grassland types, forming a fire-mediated mosaic. Reduction of fire after 1900 has led to the transformation of the parkland mosaic

of ponderosa pine and western larch to closed-canopied, Douglas-fir forest. Resource planning that includes efforts to reconstruct or mimic presettlement pine-larch conditions, such as has been planned for Pattee Canyon (USDA Forest Service 1989), will benefit from efforts to quantitatively document succession and other vegetation changes. Evaluation of GLO survey notes represents a suitable method of assessing historic vegetation change, providing reference points for vegetation management.

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and

Ponderosa Pine and Understory Growth Following Western Juniper Removal

Abstract

Recent expansions of western juniper are of great concern to land managers throughout the drier regions of the Pacific Northwest. While removal of western juniper has been found to significantly increase understory plant biomass, little information is available on the effect of western juniper removal on the tree species. This research evaluated response of understory plant biomass and cover, and ponderosa pine growth following removal of western juniper. Study sites were established in the ponderosa pine/western juniper ecotone of central Oregon. Total understory plant biomass and cover increased in response to western juniper removal. However, thinning ponderosa pine and leaving western juniper reduced biomass and cover of understory groups below control levels. Ponderosa pine under 5 cm DBH (Diameter at Breast Height) had greater percent growth in the control, where no trees were removed, than trees in treatments where competing trees were removed. Removal of western juniper appears to benefit understory vegetation, but may depress growth of small ponderosa pine trees for the first few years following tree removal.

Introduction

Encroachment of woody plants into productive shrub-steppe communities with reduction in aboveground net primary production, biological diversity, top soil, and water yields is an important challenge to many land managers throughout the western United States. In central and eastern Oregon, western juniper (*Juniperus occidentalis* Hook.) has doubled its range over the past 80 to 100 years (Caraher 1978). Western juniper's highly competitive nature allows it to invade and dominate plant communities regardless of present site conditions (Burkhardt and Tisdale 1969, 1976, Eddleman 1983, Young and Evans 1981). The increase in western juniper density is usually accompanied by reductions in understory plant biomass (Bedell 1987, Bedell and Bunch 1978, Burkhardt and Tisdale 1976, Caraher 1978, Eddleman 1987, Evans 1984).

Prior to the 1800s western juniper distribution ranged from the edge of the sagebrush steppe to the ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws) forest and occasionally into higher elevation Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands (Fowells 1965). The majority of western juniper trees were limited to rocky ridge tops and areas with shallow rocky soils throughout much of this range (Driscoll 1964). Periodic wildfires and the presence of competitive taxa on more mesic sites limited western juniper to these rocky sites. Recent fire suppression, poor grazing management,

and subtle climatic shifts have been cited as causes for the recent western juniper encroachment (Burkhardt and Tisdale 1976, Driscoll 1964, Eckert 1957, Mehringer and Wigand 1987, Vasek 1966, Young and Evans 1981). These factors may have worked separately or in combination to cause western juniper numbers to increase.

Attention has been focused on the encroachment of western juniper into the drier sagebrush-grassland. Understory plants have generally responded favorably to overstory removal of western juniper (Evans 1984, Vaitkus 1986). No information is available on the effect of western juniper on other trees. It is not known if removal of western juniper in the ponderosa pine-western juniper ecotone will increase growth of ponderosa pine on these marginal sites. The objectives of this study were to: 1) determine the effects of ponderosa pine thinning and western juniper removal on ponderosa pine; and 2) determine the effect of western juniper removal and ponderosa pine thinning on understory vegetation.

Methods

Site Description

Two study sites were located on private land in Crook County, Oregon, near Prineville. The primary site (One) was 26 km southeast of Prineville on a north to northeast facing slope above Comb's Flatt (44° 15' N, 120° 45' W). A second study site (Two) was established 33 km northwest of

Prineville on a south facing slope above Lytle Creek, east of Grizzly Mountain (44° 25' N, 121° 55' W). Sites were selected and established in an ecotone between western juniper woodland and ponderosa pine forest (Franklin and Dyrness 1973). Western juniper dominates these sites. Absence of mature juniper on the sites indicate that a majority of the trees probably established during the last 50 to 60 years when the junipers were actively expanding their range (Eddleman 1987).

Shrub species were similar on both sites. Dominant shrubs were antelope bitterbrush (*Purshia tridentata* (Pursh) OC) (nomenclature follows Hitchcock and Cronquist 1978). Mountain big sagebrush (*Artemisia tridentata* ssp. *vayseyana* (Rydb.) Beetle), Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle), and wax currant (*Ribes cereum* Dougl.). Other less abundant shrubs were low sage (*Artemisia arbuscula* Nutt.), grey rabbitbrush (*Chrysothamnus nauseosus* (Pall.) Brit.), green rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.), snowberry (*Symphoricarpos albus* (L.) Black), and serviceberry (*Amelanchier alnifolia* Nutt.).

Understory vegetation of Site One was dominated by bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith), Idaho fescue (*Festuca idahoensis* Elmer), prairie junegrass (*Koeleria cristata* Pers), bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) J.G. SM), and Sandberg bluegrass (*Poa sandbergii* Vasey). Site Two contained all of the above perennial grasses, but at lower densities. Cheatgrass (*Bromus tectorum* Vasey), six-weeks fescue (*Festuca octiflora* Walt.), and annual agrostis (*Agrostis interrupta* L.) were abundant species on site Two. Site Two also had the annual forbs, autumn willowweed (*Epilobium paniculatum* Nutt. Ex T. & G.), blepharipappus (*Blepharipappus scaber* Hook.), and tarweed (*Madia glomerata* Hook.) at higher densities than Site One.

Soils in the area were formed from weathered volcanic parent material. Soils of Site One were classified as clayey, montmorillonitic, frigid Lithic Argixerolls (Pommerining 1983). Site Two had a mixture of deep and shallow soils. These soils were classified by Pommerining (1983) as sandy, mixed, frigid, Aridic Haploxerolls and could be found mainly on foot slopes. Loamy, skeletal, mixed, frigid Pachic Haploxeroll soil was found on the midslope and slope shoulders.

Experimental Design

Four 0.4 ha treatments were established in 1984: 1) Control—no treatment; 2) Pine Thinned—pine thinned and western juniper left at pretreatment densities; 3) Juniper Removed—juniper removed and ponderosa pine left at pretreatment densities and; 4) Pine Thinned and Juniper Removed—pine thinned and all juniper removed. The treatments were applied in a randomized block design, with four blocks and four treatments. Three of the four blocks were placed on Site One. The fourth block was placed at Site Two. All ponderosa pine thinning was to an average 5.5 m x 5.5 m spacing (336 trees ha⁻¹).

Diameter at breast height (DBH) of all trees were measured prior to treatment and ponderosa pine was measured again in the fall of 1985 and 1986. Diameter was converted to basal area. Basal area growth for each pine was converted to percent growth by dividing current years growth by total tree basal area, including current year's growth. Percent growth values were used in analysis.

In 1985, understory response to western juniper removal and ponderosa pine thinning was determined from herbaceous biomass in each treatment. One hundred 0.2m² (50 cm x 40 cm) quadrats were clipped in each treatment. In each quadrat, herbaceous vegetation was clipped to 1 cm height and current years growth was clipped from shrubs. Plots were clipped during the late spring and summer to estimate peak standing crop.

In 1986, cover was used to determine understory response to treatment in addition to biomass. Cover was determined ocularly from 0.2 m² quadrats following methods outlined by Anderson (1986). An undetermined number of yearlings steers accidentally grazed blocks two and three on Site One in the spring of 1986. The steers were on the site for approximately three weeks. At the point of discovery the steers were removed, but a significant amount of the current years growth had been removed. Plant biomass was collected on the ungrazed blocks in 1986. Cover of grasses and forbs was collected and aboveground biomass from blocks where no grazing occurred. Plots that had not been grazed were clipped as in 1985 after cover estimation was complete. A simple linear regression was run on biomass and cover to compare understory response (SAS 1986).

Understory biomass and ponderosa pine growth responses were analyzed using analysis of variance.

Because of missing values the ANOVA functions from PROC GLM of SAS were used (SAS 1986). Significantly different means were separated using a Student-Newman-Keuls test at $P \geq 0.05$ (Steel and Torrie 1980).

Results

Understory Plant Response 1985

Understory biomass in all treatments was dominated by grasses and forbs. Total understory biomass in 1985 ranged from 320 to 542 kg ha⁻¹ (Table 1). Total understory, total grass, and perennial grass biomass in the Juniper Removed treatment was greater than the Pine Thinned treatment, but Pine Thinned, Control and Pine Thinned/Juniper Removed treatments were not different.

Perennial grass biomass significantly exceeded annual grass biomass in all treatments. Perennial grass biomass was dominated by bluebunch wheatgrass, Idaho fescue, bottlebrush squirreltail, and Sandberg bluegrass. Biomass of perennial grasses in the Juniper Removed treatment was greater than the Control or Pine Thinned treatments. Treatment did not affect biomass of bluebunch wheatgrass,

Idaho fescue or forbs. Bottlebrush squirreltail biomass was increased by the Juniper Removal treatment, but not significantly affected by the other treatments. Sandberg bluegrass in the Pine Thinned and Juniper Removed treatments had greater biomass than the Control or Pine Thinned/Juniper Removed treatments. Total annual grass biomass in the Juniper Removed treatment was greater than the biomass of annual grasses in the ponderosa pine thinned treatment. There was no difference in total annual grass biomass between the Control and the treatments where western juniper removal occurred. Total shrub biomass in treatments where western juniper had been removed was greater than treatments with western juniper present.

Understory Plant Response 1986

Understory herbaceous plant biomass was estimated from regression equations derived from biomass and cover data from blocks 2 and 4. There was a strong relationship between biomass and cover, $r^2 = 0.88$, $p \geq 0.05$ for total understory production (Table 2). Biomass and cover were also

TABLE 1. Understory plant biomass by treatment one year after treatment.

	Treatments			
	Control	Pine Thinned	Juniper Removed	Pine Thinned/ Juniper Removed
Species	kg ha ⁻¹	kg ha ⁻¹	kg ha ⁻¹	kg ha ⁻¹
Bluebunch wheatgrass	50.7	47.8	51.7	70.2
Idaho fescue	40.4	32.9	20.5	41.2
Bottlebrush squirreltail	17.7ab*	5.6a	42.0b	19.2ab
Sandberg bluegrass	24.2a	40.6b	47.1b	29.1a
Other perennial grasses	13.3	11.8	18.8	16.6
Total perennial grasses	146.3a	138.6a	209.9b	176.1ab
Total annual grasses	12.9ab	5.6a	28.5b	21.3ab
Total grasses	159.2a	144.2a	238.4b	197.5ab
Perennial forbs	100.2	67.2	91.5	65.7
Annual forbs	112.5	72.8	119.9	87.0
Total	212.8	140.0	211.4	152.7
Big sagebrush	20.0	32.7	51.8	31.5
Total shrubs	35.5ab	36.3a	92.3b	57.3ab
Total	407.5ab	320.5a	542.0b	407.5ab

*Different letters denote significant differences ($p \geq 0.05$) between treatments, using Student-Newman-Keuls multiple range test.

TABLE 2. Estimates of plant biomass for 1986 using regression equations derived from plant biomass and cover estimates.

Species	Treatments				r ²
	Control kg ha ⁻¹	Pine Thinned kg ha ⁻¹	Juniper Removed kg ha ⁻¹	Pine Thinned/ Juniper Removed kg ha ⁻¹	
Bluebunch wheatgrass	97.2	44.4	140.7	125.2	0.89
Idaho fescue	0.0	2.3	4.8	3.5	0.82
Total perennial grasses	178.0	106.8	251.1	245.5	0.78
Total grasses	96.7	54.6	141.0	137.7	0.90
Perennial forb	107.3	97.9	186.8	109.2	0.72
Total	339.4	241.5	462.2	422.6	0.88

TABLE 3. Two year mean percent basal area growth of all ponderosa pine and ponderosa pine in five diameter classes. Percent basal area growth equals current year basal area growth divided by total tree basal area.

All Trees	Treatments				r ²
	Control %	Pine Thinned %	Juniper Removed %	Pine Thinned/ Juniper Removed %	
1985	1.0	0.8	1.1	1.7	
1986	1.6	0.3	1.6	1.1	
Total	2.6	1.1	2.7	2.8	
Diameter Classes					
Less than 5 cm	45.1a*	21.2bc	19.0c	29.8b	
5 cm to 15 cm	5.0	5.6	9.6	8.8	
15 cm to 50 cm	3.1	4.3	10.9	4.4	
30 cm to 40 cm	4.2	2.0	2.5	2.8	
Greater than 40 cm	1.5	0.9	1.6	2.2	

* Different letters denote significant differences ($p \geq 0.05$) between treatments, using Student- Newman-Keuls multiple range test.

significantly correlated from the functional groups, perennial forbs, total grass, and total perennial grass. Estimates of biomass were highest in the Juniper Removed Treatment and lowest in the Pine Thinned treatments. This trend is similar to estimates of understory biomass one year after western juniper removal and ponderosa pine thinning.

Ponderosa Pine Growth Response

There was no significant differences in percent basal area growth due to treatment when all trees were considered (Table 3). Ponderosa pine under 5 cm DBH were the only group to exhibit a significant response to treatment. Trees in the smallest size class had significantly greater percent basal area growth in the Control than in other treatments (Table 3).

Discussion

Understory Biomass and Cover

Western juniper may be the most important competitor of understory plants in juniper/pine ecotone. Total understory biomass was estimated to be higher in the treatments where western juniper was removed. This pattern is similar to basal area response of ponderosa pine, perhaps indicating similar factors influenced both understory and pine response.

Established dominant understory plants on site before treatment were the groups to show the greatest response to western juniper removal. Other studies in central Oregon have found that removal of western juniper increased understory biomass (Bedell and Bunch 1978, Vaitkus 1986, Vaitkus and Eddleman 1991). Perhaps the perennial plants

have the ability to rapidly utilize additional resources made available by tree removal. Established perennial grasses, with fibrous root systems, and their ability to quickly produce leaf area have been found to respond quickly to tree removal. However, this response may be short lived.

Shrub biomass was also highest in treatments where western juniper had been removed. Big sagebrush, a semi-evergreen shrub, is capable of photosynthesis early in spring when most other plants are drawing on reserves to produce leaves (Miller 1988). The deep roots of big sagebrush also permit it to utilize deep water unavailable to many understory plants (Abbott *et al* 1991, Reynolds and Fraley 1989). Sagebrush biomass was lowest in the control, indicating it may have been in competition with ponderosa pine and western juniper. Shrub species appear to have responded to the Pine Thinned treatment indicating release from competition.

Ponderosa Pine Growth Response

Ponderosa pine trees under 5 cm DBH exhibited a negative response to all treatments. The small trees were most often found under the canopy of another larger woody plant. In a study of western juniper, over 90 percent of the juvenile western trees found were beneath the canopy of larger juniper or mountain big sagebrush (file data, EO-ARC). It is thought that this location provides the juvenile trees with a more moderate microclimate than in the interspace areas where they are exposed to full sunlight. A similar condition may occur with the younger ponderosa pine at this dry end of its range. Removing the overstory trees exposes the smaller trees to greater microclimate fluctuations than experienced under the canopy of a larger tree or shrub. The smaller trees may need time to adjust to the more direct sunlight and greater temperature fluctuations. Shrub and grass biomass also increased following tree removal and may increase competition with smaller ponderosa pine trees.

Other studies of dense stands of larger ponderosa pine have reported a lag in response to thinning (Barrett 1982, Brix and Mitchell 1986, Oliver 1979, Oren *et al.* 1987). The high initial tree densities in this study, 988 trees ha⁻¹ (western juniper and ponderosa pine), may also have contributed to the thinning response lag. Delayed response has been attributed to many factors. One of the first consequences of thinning is an increase

in root and leaf area of residual trees (Perry 1985). The lag in basal area growth could be caused by the larger trees adding substantial levels of new needles. Roots may need time to grow into areas left vacant by removed trees. Brix and Mitchell (1986) found that root systems of Douglas-fir left after thinning might not be sufficient to absorb the additional moisture.

Oren and others (1987) found that diameter increases of ponderosa pine at lowest stocking densities was over twice that of pine in the highest stocking densities. Growth of ponderosa pine in dense stands after light thinning was found by Oliver (1979) to be below the pre-thinning level in northeastern California. Removing western juniper may be comparable to heavy thinning of ponderosa pine. Far greater numbers of potential competitors were removed (250-300 ha⁻¹) from the stand when western juniper was removed, while an average of 53 trees ha⁻¹ were removed in treatments where ponderosa pine was thinned. Increased exposure of crowns after thinning and insufficient root area may lead to greater transpiration and moisture stress for the tree resulting in little initial growth response after tree removal.

Thinning of ponderosa pine may not be economically practical, especially if western juniper is not treated. Western juniper's aggressive nature may allow it to capitalize on resources made available by thinning, leaving little available for remaining ponderosa pine. Short term thinning response observed in this study indicates that additional growth of residual ponderosa pine would never replace the potential future growth and volume of trees removed during thinning.

Evaluating two years post treatment response may not be enough to determine the effects of ponderosa pine thinning and western juniper removal on residual ponderosa pine growth. However, the understory vegetation did positively respond to western juniper removal and/or ponderosa pine thinning one year after treatment. Less than 11 km away a study conducted in Crook County (Vaitkus 1986, Vaitkus and Eddleman 1991) found that removal of western juniper increased understory biomass markedly the first and second year following western juniper removal. Precipitation is lower on this site and no ponderosa were present. Sandberg bluegrass and perennial forb biomass differed slightly from areas with western juniper present treatments. Release from moisture competition with western juniper seemed to be the

most important factor on these sites (Vaitkus and Eddleman 1991).

Thinned stands are often used as a transitory range until canopy closure occurs and forage biomass falls below usable levels. Thinning for increases in livestock forage alone is often impractical, but when considered as an adjunct to timber improvement, increases in forage yields could become an important part of a farm/forestry program (McConnell and Smith 1970). Conversely, timber values of sparsely forested areas are often overlooked because of their value as spring, fall, and summer range for domestic livestock. Coordination of management objectives could increase the economic value of these areas.

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Ben F. Roché, Jr., Department of Natural Resource Sciences, Washington State University, Pullman, Washington 99164-6410

Cindy T. Roché, Department of Plant, Soil, and Entomological Sciences, University of Idaho, Moscow, Idaho 83844-2339
and

Roger C. Chapman, Department of Natural Resource Sciences, Washington State University, Pullman, Washington 99164-6410

Impacts of Grassland Habitat on Yellow Starthistle (*Centaurea solstitialis* L.) Invasion

Abstract

Yellow starthistle, a Mediterranean winter annual introduced in southeastern Washington around the turn of the century, expanded rapidly in foothills rangeland of the Blue Mountains in the early 1960s, invading and dominating bluebunch wheatgrass communities on deeper soils of south-facing slopes. Examination of site differences (soil depth and aspect) revealed a high correlation of yellow starthistle with stored soil moisture on south-facing slopes. Yellow starthistle roots grew rapidly and continuously during the winter giving it access to moisture stored deep in the soil profile not depleted by the native plant association. Yellow starthistle seedlings grown under reduced light produced shorter roots, larger leaves, more erect rosettes and fewer flowers than plants grown in full sunlight. Interaction of shade and moisture stress appeared to reduce yellow starthistle invasion of four species of perennial grass treated with four seasonal clipping regimes: May, July, October, and no clipping. The two sod forming cultivars, "Oahe" intermediate wheatgrass and "Luna" pubescent wheatgrass were generally less susceptible to starthistle invasion under all clipping regimes than the two bunchgrasses, "Nordan" crested wheatgrass and "Whitmar" bluebunch wheatgrass. Yellow starthistle invaded Whitmar bluebunch wheatgrass clipped any time of year. All four grass species resisted starthistle invasion if left unclipped. Two critical factors limiting starthistle invasion in eastern Washington appeared to be light intensity at the soil surface during the winter and residual soil moisture during the summer.

Introduction

Yellow starthistle, a facultative winter annual native to the Mediterranean region, is a serious rangeland weed in the western United States (Maddox *et al.* 1985), occupying an estimated 3.7 million ha (Roché and Roché 1991). The first permanent record of yellow starthistle in Washington is an herbarium specimen collected from Seattle in 1898 (Roché and Talbott 1986). Within 10 years, residents of Whiskey Creek drainage of Columbia and Walla Walla counties in southeastern Washington found yellow starthistle in an alfalfa seeding (Roché 1965). After an initial lag period, populations appeared to explode on rangeland in Columbia County, expanding from 60 ha in 1954 to 4,000 ha in 1964 (Roché 1965). Ranchers' fears that yellow starthistle would soon dominate the foothill rangeland of the Blue Mountains of Washington and Oregon prompted studies of yellow starthistle ecology to identify environmental limits to its expansion, and life history characteristics that would provide options for its containment. Unfortunately, yellow starthistle populations continued to expand on Pacific Northwest rangelands (Roché and Roché 1988) and currently receive major emphasis in both county and state level weed control programs.

Vegetation of the natural grasslands in southeastern Washington becomes dormant in summer, avoiding seasonal water stress. In striking contrast, yellow starthistle remains vigorously active, flowering and producing seed in July and August in these communities. In theory, if the native bunchgrass community depletes the soil moisture in the process of completing its growth cycle by early summer as described by Daubenmire (1940), drought would restrict seed production in yellow starthistle, giving the competitive edge to the perennials. Clues to interpreting yellow starthistle's successful invasion of these bunchgrass rangelands appeared to lie in the distinct spatial pattern of yellow starthistle dominance on southeast to southwest-facing slopes, especially areas of moderate to deep silt loam soils and its conspicuous absence on north-facing slopes or sparse stands on shallow soils (Roché 1965).

Beginning with the pattern of yellow starthistle invasion in southeastern Washington, this paper reports a series of observations and studies conducted from 1963 through 1974 on the biology and ecology of yellow starthistle. These included the behavior of yellow starthistle roots during establishment (winter 1966-67), the response of

yellow starthistle to reduced light (winter 1969-70), and the differences in yellow starthistle invasion of established perennial grasses under different management systems (1971-74).

Methods and Materials

Natural communities: sites and observations

Natural plant communities in Payne Hollow, Columbia County, Washington, were used to investigate the pattern of invasion of a vegetational mosaic within the *Agropyron-Festuca* zone (Daubenmire 1970) in the foothills of the Blue Mountains. Hot, dry summers characterize the area, and winters are comparatively mild for the latitude (46° 15' N). Average long-term annual precipitation (1901-1960) was 49.6 cm, with 92% received October through June (Phillips 1970). Within the *Agropyron-Festuca* zone, xeric sites support the *Agropyron-Poa* association and cooler, more mesic sites are dominated by rose (*Rosa* spp.) and snowberry (*Symphoricarpos albus*) (Daubenmire 1970).

The Payne Hollow site was situated at an elevation of 525 m between two cultivated fields, approximately 5 ha fenced separately and historically grazed only occasionally. The soil series was mapped as an Athena silt loam (fine-silty, mixed, mesic Pachic Haploxerolls) (Harrison *et al.* 1973). The soils in the study area appeared as intergrades within the series, including lithosols on the shallow end. Because the mosaic included shallow soils, the study site had never been cultivated. Soil depth

and development varied from 12 cm with an undifferentiated profile to 152 cm with well-developed horizons. A soil probe was used to select 10 stands within this range of soil depths which had relatively uniform within stand soil depth. Size and shape of stands were not uniform, but ranged in size from 50 to 200 m in width and length. Slope and aspect were recorded for each stand, ranging from south 3° west to south 59° east on 32 to 50% slopes (Table 1). To determine seasonal water potential changes, two soil samples were analyzed from three random locations within each stand, at 15 cm depth intervals, on 19 May, 2 July and 29 August 1963. Water potentials were determined using standard pressure membrane procedures (Richards 1941) and water content determined gravimetrically. Water content was also determined at -1.5 MPa for samples taken 19 May and 2 July as a rough estimate of state of soil moisture availability to plants.

On 4 April 1963 cover and frequency of yellow starthistle and bluebunch wheatgrass were estimated on 25 plots that measured 2 by 5 dm equally spaced across the longer dimension of each stand, using the canopy-coverage method of Daubenmire (1959). In addition, yellow starthistle density was estimated on half of each plot (2 by 2.5 dm) on 4 April and again on 7 July.

To determine rooting habit and depth of penetration, roots of 10 randomly selected yellow starthistle plants were carefully excavated from deep soil profiles on each of three dates (4 April, 6 July and 28 August).

TABLE 1. Topographic features, soil depth, cover and frequency of bluebunch wheatgrass and yellow starthistle in 10 stands in Payne Hollow, Columbia County, Washington on 4 April 1963, and starthistle density on 7 July 1963.

	Stand									
	1	2	3	4	5	6	7	8	9	10
Aspect	S22E	S22E	S27E	S6E	S59E	S59E	S28E	S9E	S3W	S7E
Slope (%)	42	50	42	41	46	36	41	41	32	35
Soil depth (cm)	12	20	30	46	84	86	98	117	122	122
Bluebunch wheatgrass										
cover (%)	13	33	18	17	40	24	29	2	4	7
frequency (%)	64	80	72	80	96	60	87	12	24	24
Yellow starthistle										
cover (%)	1	6	6	11	16	31	35	27	33	36
frequency (%)	32	100	68	80	100	100	100	100	100	100
density (April) no./0.05m ²	2	10	3	12	17	23	30	27	51	35
density (July) no./0.05m ²	0.4	4	2	6	9	15	10	11	12	9
Survival (%)	18	43	70	49	53	63	34	40	23	26

To investigate aspect influences, another study area was selected at the Payne Hollow site where a knife-edge ridge extending east to west provided an abrupt transition from north- to south-facing slopes. The northerly aspect was dominated by Idaho fescue (*Festuca idahoensis*), while the southerly aspect, normally dominated by blue-bunch wheatgrass, was occupied by yellow starthistle. Observations of yellow starthistle density and soil moisture were recorded in April, June, July and August 1963.

Evaluation of factors with artificially established plants

Three studies to test observations in natural communities, including root elongation, response to shade, and invasion of established perennial grass stands, were conducted at the Steffen Research Center at Pullman, Washington, on a south-facing (186°) 5 to 20% slope. The soil was a Palouse silt loam (fine-silty, mixed, mesic Pachic Ultic Haploxerolls) (Donaldson 1980). Average long term annual precipitation was 52 cm, with 90% received October through June (Phillips 1965).

Root elongation study

To observe the rate of root elongation and rosette development in yellow starthistle, plants were grown in 52 mm x 123 cm Pyrex tubes. These were inserted in metal sleeves buried in the soil at a 22.5° angle from vertical. Tubes were filled with silt loam soil from the site. On 26 October 1966, germinated plumed and plumeless yellow starthistle seeds were planted in the top of separate tubes, each replicated 10 times. The tubes were lifted to record root length and rosette diameter on successive dates throughout winter and early spring (Table 5). On 10 June, plants were removed from the tubes by gently flushing the soil from the tubes with a slow stream of water, then tops and roots were oven dried and weighed.

Shade study

To study the effect of light reduction on yellow starthistle, plants were grown under tents of Saran cloth¹ which reduced ambient light levels to 70, 53, 45, 37, 27, 20 and 6% of full sunlight. A-frame tents 183 cm long were constructed with a continuous vent along the top, one end open and

the opposite end equipped with a small electric fan for air ventilation. Tents were situated with the lengthwise dimension from east to west on a south-facing, 9% slope. Each treatment was replicated twice. Under each shade condition, yellow starthistle was grown in tubes to measure root growth and directly in the soil to measure plant size and flower production. Tubes were buried in rows 45 cm apart and 68 cm away from the edge of the frame, at 22.5° from vertical as in the root elongation study with 10 tubes per light level. Both direct seeding and seeding in the tubes were done on 3 October 1969. Due to the dry fall, irrigation was necessary for seed germination. Canvas soaker hoses were used to wet the soil to 1.5 cm until the seedlings emerged. The tubes were watered to replace moisture lost to evaporation in the top 5 cm. On 14 November, yellow starthistle plants were thinned to one per tube and to 15 cm apart within rows in the direct seeding, and the shade tents were set over the plants. On 18 November 1969 and 24 March 1970, root length, size of largest leaf, and distance from that leaf to the ground were measured on tube-grown plants. On 7 July 1970, the height, rosette area and number of flowers per plant were recorded for direct seeded plants, which were then harvested. Weight of above ground biomass was recorded for oven dried plants.

Invasion of seeded grass

Four species of rangeland forage grasses were established in plots 2.7 x 2.7 m by seeding 4.7 cm spaced rows during the fall of 1970. These included two sod forming species, Oahe intermediate wheatgrass and Luna pubescent wheatgrass (*Elytrigia intermedia* (Host) Nevski), and two bunchgrasses, Nordan crested wheatgrass (*Agropyron desertorum* (Fisch. ex Link) Schultes) and Whitmar bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love ssp. *inermis* (Scribner & Sm.) A. Love). Nomenclature for grass cultivars follows U.S.D.A. Soil Conservation Service (1992). The four management treatments included clipping at one of three times (May, July, October) and no clipping, simulating light conditions under a canopy of grazed at boot stage, grazed after flowering, grazed at ripe-seed stage, and not grazed. Each treatment was replicated 4 times in a randomized complete block design. Clipped plots were cut to 10 cm height with a GravelyTM mower, except the center m² of each plot in which the grass was hand clipped, leaving the yellow starthistle plants

¹Chicopee Manufacturing Company, Cornelia, Georgia

unclipped. The clipping regime began fall of 1971 and continued through summer 1974. Each fall beginning in 1971, yellow starthistle seeds were planted 2 cm apart between the center three rows of each plot of the established grasses. The number of seeds available for potential establishment did not remain uniform through the study period because some additional seed was produced by successful yellow starthistle plants in 1972 and 1973. This pattern approximates natural conditions of yellow starthistle invasion.

The number of yellow starthistle plants in each plot was recorded on 1 October 1973, and 21 April and 13 September 1974. General observations of starthistle height, phenology and seed production were also recorded. No data were recorded for 1972 because of severe rodent damage to the plots.

Statistical analyses

The strength of the associations between starthistle cover and soil depth and moisture, and plant response to light reduction were quantified using Pearson's correlation coefficient. Student's *t*-test was used to compare mean root lengths, rosette diameter and biomass between seedlings from plumed and plumeless seeds in the winter root elongation study. In grass variety experiments, statistical comparison of means with unequal variances and unequal sample sizes was done using Tukey's Honestly Significant Difference Test (Toothaker 1993, Klockars and Sax 1986).

Results and Discussion

Observations in natural communities

In the absence of major environmental disturbances, yellow starthistle had invaded and dominated bluebunch wheatgrass communities on the deeper soils of southeast- to southwest-facing slopes in Payne Hollow. Yellow starthistle cover was positively correlated ($r=0.94$, $P\leq 0.001$) with increasing soil depth (Table 1).

Differences in phenology between bluebunch wheatgrass and yellow starthistle in the study area were striking. On 19 May, bluebunch wheatgrass was flowering and yellow starthistle plants were still small rosettes, 7 to 13 cm in diameter. On 2 July, the bluebunch wheatgrass bore mature seed heads, retaining some yellow-green color only in the lower portions of the bunch whereas yellow starthistle was

just entering its reproductive stage, with fewer than 1% of the heads showing yellow flowers. On 29 August, except for shrubs and yellow starthistle, the vegetation had matured and was dormant. Yellow starthistle was still producing a few flowers, although most heads were maturing and dispersal of plumed seeds had begun.

Excavation of yellow starthistle roots from deep soil sites revealed a consistent rooting pattern. Each seedling root developed one primary taproot with short secondary branches. By 4 April, taproots of fall-germinated yellow starthistle plants exceeded 30 cm, although rosettes remained less than 6 cm in diameter. On 6 July, plants growing on deep soil, averaging 25 cm tall, had taproots with a mean depth of 66 cm. The unbranched primary root habit continued through the growing season until 28 August, when the primary taproot was observed to have branched where it reached broken rock 91 cm below the soil surface. On shallow soil sites, root depth was restricted by rock.

In the ten stands on the south-facing slope, yellow starthistle cover and density were related to soil moisture. Cover of yellow starthistle was highly correlated with total soil moisture on 19 May ($r=0.93$, $P\leq 0.001$), on 2 July ($r=0.92$, $P\leq 0.001$) and on 29 August ($r=0.95$, $P\leq 0.001$) (Tables 1 to 4). Correlations between yellow starthistle cover and soil moisture in excess of -1.5 MPa on 19 May ($r=0.88$, $P\leq 0.01$) and 2 July ($r=0.75$, $P\leq 0.05$) were also significant. Percent survival of yellow starthistle between 4 April and 7 July did not increase with soil depth (Table 1). Density reduction was apparently due to severe depletion of soil water in the top 30 cm in all soils (Tables 2 and 3): by 19 May, only 1.6 cm water remained in the shallowest soil (12 cm) and by 2 July water in the top 30 cm of soil in all stands was held at tensions greater than -1.5 MPa. Although yellow starthistle roots undoubtedly extract soil moisture at greater tensions, these values indicate a pattern of soil moisture depletion. Because the soil water potentials from which mature yellow starthistle can extract water are not known, -1.5 MPa was used as a recognizable reference point.

Root elongation study

The rooting pattern of yellow starthistle seedlings in observation tubes was the same as roots excavated in the natural community: one main taproot with short side branches. Mean root length of

TABLE 2. Soil moisture (cm) by 15 cm depth intervals in 10 stands in Payne Hollow, Columbia County, Washington, on 19 May 1963.

Soil Depth (cm)	Stand									
	1	2	3	4	5	6	7	8	9	10
0-15	1.6	2.7	1.2	2.6	2.9	2.9	2.7	2.7	2.9	2.8
15-30		1.0	1.9	3.5	3.9	3.7	3.6	3.7	3.6	3.7
30-45				3.7	4.0	3.8	3.7	3.7	3.5	3.7
45-60					4.1	3.9	3.8	3.8	3.6	3.7
60-75					4.0	3.7	3.7	3.7	3.3	3.5
75-90					1.8	2.5	4.1	3.9	3.4	3.5
90-105							1.8	4.1	3.4	3.6
105-122								2.7	2.7	3.7
Total	1.6	3.7	3.1	9.8	20.8	20.5	23.2	28.3	26.4	28.2
-1.5 MPa	0.0	3.2	0.05	5.4	8.6	9.3	9.6	16.6	11.3	13.7

TABLE 3. Soil moisture (cm) by 15 cm depth intervals in 10 stands in Payne Hollow, Columbia County, Washington, on 2 July 1963.

Soil Depth (cm)	Stand									
	1	2	3	4	5	6	7	8	9	10
0-15	1.1	1.4	0.7	1.1	1.7	1.7	1.7	1.9	1.8	1.9
15-30		0.6	1.1	1.8	2.1	1.9	2.1	2.2	1.9	2.0
30-45				3.0	2.1	2.0	2.1	2.2	2.0	2.0
45-60					2.2	2.2	2.3	2.4	2.2	2.1
60-75					2.3	1.9	2.2	2.3	1.9	2.0
75-90					0.8	1.2	2.4	2.6	1.8	2.0
90-105							1.0	2.6	2.0	2.4
105-122								1.8	1.7	2.4
Total	1.1	2.0	1.8	5.8	11.3	11.0	13.8	18.0	15.3	16.7
-1.5 MPa	0.0	0.02	0.0	0.7	1.3	2.2	2.8	8.6	4.7	6.7

TABLE 4. Soil moisture (cm) by 15 cm depth intervals in 10 stands in Payne Hollow, Columbia County, Washington, on 29 August 1963.

Soil Depth (cm)	Stand									
	1	2	3	4	5	6	7	8	9	10
0-15	0.5	1.0	0.2	1.0	1.1	1.1	0.9	1.0	1.3	1.1
15-30		0.4	1.1	1.3	1.5	1.5	1.6	1.4	1.5	1.5
30-45				1.2	1.6	1.7	1.9	1.5	1.5	1.5
45-60					1.5	1.8	1.9	1.5	1.7	1.6
60-75					0.7	1.5	1.5	1.4	1.5	1.5
75-90						0.9	0.6	1.4	1.4	1.4
90-105								1.4	1.5	1.5
105-122								0.9	1.2	1.4
Total	0.5	1.4	1.3	3.5	7.9	8.4	9.8	10.5	11.6	11.5

2 month old plants exceeded 30 cm and during the next month of growth (by 19 January); they doubled their length to 67 cm. Growth of roots of plants from plumeless seed was not significantly different than those from plumed seeds ($P \leq 0.05$). On 19 January, roots of 2 plants from plumeless seeds had grow out the bottom of the 123 cm long tubes; this number increased to 5 "plumeless" roots and 2 "plumed" roots by 24 February (Table 5). By 10 April, roots of all the plants from plumeless seeds and 80% of plants from plumed seeds had exceeded the length of the tubes. Mean root growth generally exceeded 0.5 cm per day after the plants were a month old (Table 5). During March, yellow starthistle roots grew 1.0 to 2.1 cm per day (Table 5). Roots of cheatgrass (*Bromus tectorum*) seedlings grown in the same tubes at the same site in a different year (4 October 1963 to 2 June 1964) also grew rapidly during the winter but showed a different growth form: cheatgrass developed numerous adventitious roots in contrast to yellow starthistle's taproot (Harris 1965, 1967). Because cheatgrass formed normal branching in the tubes, and yellow starthistle roots in the natural community had the same form as those in the

tubes, we concluded that the tubes did not appreciably alter the rooting pattern under winter growth conditions.

Yellow starthistle's growth strategy appeared to allocate resources first to root extension, then later to leaf expansion. Rosettes grew slowly during the first 86 days, with the starting diameters of 1.1 cm (plumeless) and 1.2 cm (plumed) on 4 November increasing only to 2.6 cm (plumeless) and 2.3 cm (plumed) by 19 January (Table 5). During this time the roots extended their length more than 10 fold, from 6.1 cm to 67.3 cm. Between 19 January and 10 April, rosettes grew more rapidly, increasing to 8.4 cm. The size difference between rosettes from plumed and plumeless seeds was not significant (Table 5). Harris (1977) reported a similar pattern in cheatgrass and medusahead (*Taeniatherum asperum*), both of which grew primary roots during winter when leaves showed little growth. However, by 10 June, when starthistle began to elongate a flowering stem, aboveground biomass was significantly greater than below ground biomass ($P \leq 0.01$). Differences between plumeless (rosette 2.9 g, root 2.2 g) and plumed (rosette 2.9 g, root 2.3 g) were not significant.

TABLE 5. Mean rosette diameter and mean daily root growth of fall germinated yellow starthistle grown in tubes at Pullman, Washington, from 26 October 1966 to 10 April 1967.

Date	Age (days)	Plumed seed			Plumeless seed		
		Rosette diameter (cm)	Root growth† (cm/day)	Roots > 123 cm (%)	Rosette diameter (cm)	Root growth† (cm/day)	Roots > 123 cm (%)
4 Nov 66	10	1.1 (0.03)*			1.2 (0.04)		
8 Nov 66	14	1.2 (0.04)	0.2 (0.1)		1.2 (0.05)	0.3 (0.1)	
15 Nov 66	21	1.3 (0.04)	0.2 (0.1)		1.4 (0.04)	0.4 (0.1)	
22 Nov 66	28	1.5 (0.05)	0.3 (0.1)		1.5 (0.1)	0.5 (0.04)	
29 Nov 66	35	1.7 (0.1)	0.5 (0.1)		1.7 (0.1)	0.8 (0.1)	
8 Dec 66	44	1.7 (0.1)	0.6 (0.1)		1.8 (0.1)	0.8 (0.1)	
22 Dec 66	58	1.8 (0.1)	0.7 (0.1)		1.9 (0.1)	0.8 (0.1)	
4 Jan 67	71	1.8 (0.1)	0.6 (0.1)		1.9 (0.1)	0.7 (0.1)	
19 Jan 67	86	2.3 (0.1)	1.4 (0.2)		2.6 (0.1)	1.9 (0.3)	20
24 Feb 67	122	2.7 (0.1)	0.7 (0.1)	20	3.1 (0.1)	0.9 (0.2)	50
6 Mar 67	132	3.2 (0.02)	1.3 (0.1)	20	3.6 (0.2)	1.5 (0.1)	60
15 Mar 67	141	3.7 (0.2)	1.4 (0.2)	20	4.0 (0.2)	1.8 (0.5)	80
24 Mar 67	150	5.0 (0.2)	1.0 (0.1)	40	5.2 (0.2)	2.1 (0.1)	90
3 Apr 67	160	6.6 (0.3)	1.6 (0.5)	80	6.2 (0.3)		90
10 Apr 67	167	8.6 (0.3)	1.1 (0.4)	80	8.2 (0.4)		100

† Calculation of mean root growth per day includes only those roots which had not reached the end of the tube by the beginning of the growth period. No mean was calculated when fewer than two roots remained inside the tubes.

* Numbers in parentheses represent the Standard Error.

Availability of soil moisture at crucial times of ten determines whether plants succeed (Daubenmire 1972). Cheatgrass, a prior invader of the same grasslands, succeeded because its rapid root growth throughout the winter enabled it to avoid drought by entering summer dormancy as seeds 5 to 7 weeks earlier than bluebunch wheatgrass (Harris 1977). However, yellow starthistle's later flowering produced mature seed 6 to 8 weeks later than bluebunch wheatgrass, requiring a different strategy to overcome the summer drought. In the bluebunch wheatgrass community, the growing season which ends in early summer appears to be related to species phenology and rooting zone soil moisture depletion. In southwestern Oregon range-land communities, yellow starthistle invaded annual grasslands by utilizing residual soil moisture left by earlier maturing annuals (Borman *et al.* 1992). In the same manner, moisture in deeper soils not used by the native plant community before entering summer dormancy may allow yellow starthistle invasion in southeastern Washington.

The *Agropyron-Festuca* and *Agropyron-Poa* associations lack shrubs, except for scattered rabbitbrush (*Chrysothamnus* spp.). In grassland communities of the Great Basin and Columbia Plateau, native shrubs and forbs are deeper rooted than the large perennial bunchgrasses such as bluebunch wheatgrass (Dobrowolski *et al.* 1990). Daubenmire (1970) reported that in the drier area immediately west of the *Agropyron-Poa* zone, moisture percolated below the reach of grass roots often enough to maintain a stand of big sagebrush (*Artemisia tridentata*) through the rainless summer. From this he suspected that scattered rabbitbrush in the *Agropyron-Poa* zone indicated the existence of unused resources in the form of deeper soil moisture.

If soil moisture were the only factor in successful yellow starthistle invasion, starthistle should have invaded north-facing slopes. In spite of differences in vegetation, observations of soil moisture (total and depth distribution) on 9 June, 2 July and 29 August did not differ between the fescue-dominated north-facing slope and the starthistle-dominated south-facing slope. This observation is consistent with research by Borman and others (1992) who reported similar moisture extraction by yellow starthistle and perennial grasses to depths of 60 cm. Because yellow starthistle seed fell in the perennial grass area, aspect-related factors of

light and temperature might have influenced starthistle establishment.

Shade study

Under reduced light, seedling yellow starthistle developed large leaves in upright rosettes (measured as the distance from the tip of the largest leaf to the ground) in contrast to compact, decumbent rosettes in full light (Figure 1). Leaf size and distance to the ground were negatively correlated with light level ($r = -0.95$, size; -0.93 , distance; $P \leq 0.001$). A change in growth habit from prostrate to erect leaves in response to shade (Palmer 1956, Harper 1977) and increased leaf area has been reported for other species (Boyd and Murray 1982, Dall'Armellina and Zimdahl 1988). By 24 March, two plants under 6% light and one plant under 20% light had died. Root length correlated positively ($r = 0.94$, $P \leq 0.001$) with light level (Figure 1). Measurements made on 8 July showed that height, rosette area and above ground biomass declined with decreasing light ($r = 0.80$, height; $r = 0.91$, area; $r = 0.93$, biomass; $P \leq 0.01$) (Figure 1). Shade reduced reproductive capacity as shown by failure of plants grown under 6% full sunlight to flower. Mean number of flowers increased with light: 0.3 flowers per plant under 20-27% light; 0.6, 37-45%; 1.6, 55%; 1.1, 70%; and 6, 100%.

Prodan (1930) characterized yellow starthistle as an obligate heliophyte, probably referring to starthistle's prevalence in warm sunny habitats. In Washington, yellow starthistle rosettes appeared to exploit favorable microclimatic conditions at the soil surface on south-facing slopes, allowing it to develop rooting depth during winter while moisture is not limiting. In a study of winter annuals, Regehr and Bazzaz (1976) found that not only was rosette leaf temperature significantly higher than air temperature, but net photosynthesis was maintained even at low irradiance and temperatures down to the point of freezing of leaf tissue. In contrast, studies of bluebunch wheatgrass maintenance of photosynthetically active tissue through the winter in the Great Basin concluded that its primary function is to facilitate faster growth in the early spring (Nowak and Caldwell 1984). Yellow starthistle accumulated enough energy during the winter to grow actively, especially in root development. Photosynthesis by starthistle rosettes on north-facing slopes would be reduced directly by lower irradiance and indirectly by lower leaf temperatures,

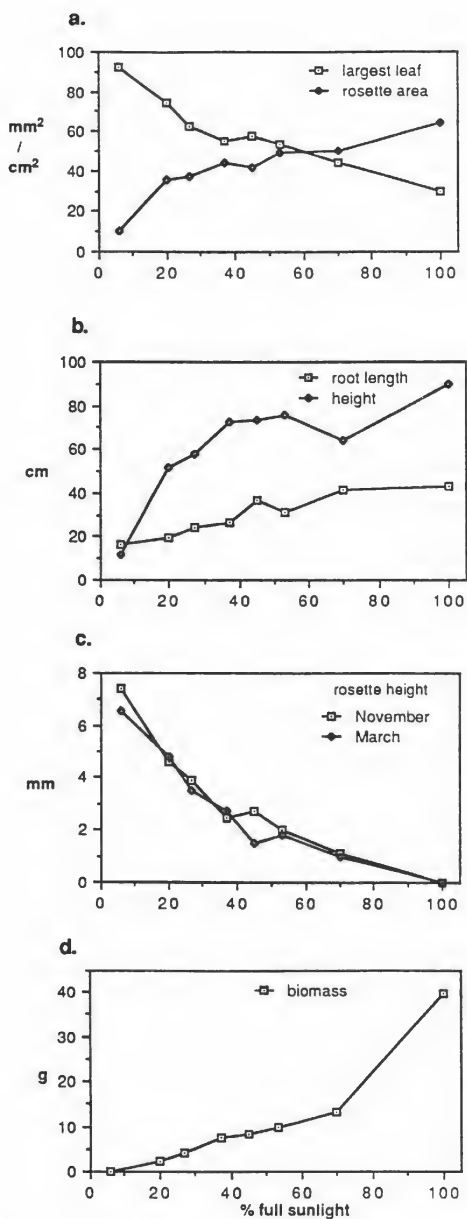


Figure 1. Trends of plant characteristics of yellow starthistle grown under shade tents in Pullman, Washington: a) size of largest leaf in mm² and rosette area in cm² on 18 November; b) root length in cm on 18 November and plant height in cm on 7 July; c) distance from rosette leaf to ground in mm on 18 November and 24 March; and d) total above ground biomass in g on 7 July.

which likely accounts for failure to invade native vegetation on the north aspect in Payne Hollow.

Dillon (1967) reported dramatic differences in natural revegetation of north- and south-facing steep (65%) slopes in Walla Walla County. In 1901, a railroad fill was constructed of silt loam soil and livestock were fenced out. Sixty-four years later, the north-facing slope was 80% bluebunch wheatgrass and 20% Sandberg bluegrass (*Poa sandbergii*), while the south-facing slope was dominated by annuals: 60% cheatgrass, 30% *Centaurea* (yellow starthistle) and 5% tumble mustard (*Sisymbrium altissimum*).

Invasion of seeded grass

In 1973 no yellow starthistle plants invaded any of the established perennial grass varieties that were not clipped (Table 6). Levels of yellow starthistle invasion were not significantly different in fall and summer clipping of the sod-forming grasses and spring clipping of Luna pubescent wheatgrass (Table 6). Clipped bunchgrasses were much more susceptible to invasion than the sod-forming grasses. Yellow starthistle was particularly successful in spring or fall clipped Whitmar bluebunch wheatgrass. Observations of plant size, relative vigor and seed production revealed that yellow starthistle in the sod-forming grasses were smaller, weaker and produced less seed. However, plants that survived to October produced some seed.

In 1974 counts of yellow starthistle plants in April and September showed high mortality during the summer (Tables 7 and 8). Although starthistle seedlings were present in all treatments in April, the number remaining in September 1974 in the unclipped plots was similar to the number in fall 1973. Summer and fall clipping of the sod-forming species allowed less starthistle survival than spring clipping (Table 8). Whitmar bluebunch wheatgrass clipped during any season was susceptible to invasion, as was Nordan crested wheatgrass clipped during spring or summer and Luna pubescent and Oahe intermediate wheatgrasses clipped in the spring (Table 8). In April yellow starthistle seedlings in plots shaded by grass litter and standing crop appeared weak and spindly with erect yellowish-green leaves compared to vigorous blue-green leaves of prostrate rosettes grown in grass-free control plots. The rosette growth form is particularly vulnerable to shading by overtopping vegetation (Regehr and Bazzaz 1976). The similarity

TABLE 6. Mean number of yellow starthistle plants in the center m² of seeded grass variety plots $\pm$ Standard Deviation (S.D.) by clipping regime on 1 October 1973.

Grass	Clipping Regime			
	None	Fall	Summer	Spring
Luna	0a	5.0 $\pm$ 9.3a	5.0 $\pm$ 7.1a	1.8 $\pm$ 2.9a
Oahe	0a	6.8 $\pm$ 6.2a	4.8 $\pm$ 3.2a	7.5 $\pm$ 5.3a
Nordan	0a	17.0 $\pm$ 7.6bc	10.3 $\pm$ 8.4abc	21.8 $\pm$ 14.2cd
Whitmar	0a	26.3 $\pm$ 19.7bcde	17.5 $\pm$ 17.1bcd	31.8 $\pm$ 23.4e

Means are compared across rows and columns so that those followed by the same letters anywhere in the table are not significantly different, as determined by the HSD test at the 5% level of significance.

TABLE 7. Mean number of yellow starthistle plants in the center m² of seeded grass variety plots $\pm$ Standard Deviation (S.D.) by clipping regime on 21 April 1974.

Grass	Clipping Regime			
	None	Fall	Summer	Spring
Luna	20.5 $\pm$ 14.2b	73.8 $\pm$ 92.9e	53.0 $\pm$ 73.6c	84.8 $\pm$ 33.1f
Oahe	51.8 $\pm$ 82.9c	76.5 $\pm$ 51.2e	61.5 $\pm$ 38.5d	52.5 $\pm$ 62.9c
Nordan	11.5 $\pm$ 12.2a	85.5 $\pm$ 105.7f	85.0 $\pm$ 42.1f	51.5 $\pm$ 30.8c
Whitmar	5.3 $\pm$ 1.7a	64.3 $\pm$ 51.7d	55.8 $\pm$ 62.3cd	70.0 $\pm$ 71.5de

Means are compared across rows and columns so that those followed by the same letters anywhere in the table are not significantly different, as determined by the HSD test at the 5% level of significance.

TABLE 8. Mean number of yellow starthistle plants in the center m² of seeded grass variety plots $\pm$ Standard Deviation (S.D.) by clipping regime on 13 September 1974.

Grass	Clipping Regime			
	None	Fall	Summer	Spring
Luna	1.0 $\pm$ 1.5a	7.0 $\pm$ 12.1ab	0 $\pm$ 0a	30.8 $\pm$ 25.3e
Oahe	0.5 $\pm$ 0.6a	1.0 $\pm$ 2.0ab	0.8 $\pm$ 1.5a	14.8 $\pm$ 11.2bc
Nordan	0.3 $\pm$ 0.5a	5.8 $\pm$ 10.8a	30.0 $\pm$ 1.5e	44.0 $\pm$ 32.9ef
Whitmar	0.8 $\pm$ 1.5a	43.3 $\pm$ 36.7ef	19.3 $\pm$ 33.5d	59.7 $\pm$ 50.8g

Means are compared across rows and columns so that those followed by the same letters anywhere in the table are not significantly different, as determined by the HSD test at the 5% level of significance.

of yellow starthistle seedlings in unclipped perennial grass stands to plants grown under tents implicated shade as the stress factor. The failure of starthistle seedlings to develop normal rooting depth under shade tents implicated drought stress as the reason starthistle seedlings died between April and September in perennial grass stands on deep silt loam soil. Unfortunately, direct comparison of shade conditions could not be made because equipment to appropriately measure photosynthet-

ically active radiation (Patterson 1979) was not available for the study.

Conclusions

A survey of the distribution of the 54,000 ha of yellow starthistle in eastern Washington (Roché and Roché 1988) suggested that the factors identified in the Payne Hollow study may be important determinants for starthistle invasion over a broader area of eastern Washington. The North American

yellow starthistle invasion that reaches its supremacy in California (Maddox *et al.* 1985) appears to approach the northern limits of its ecologic amplitude at 48° 45' N Lat. in northeastern Washington (Talbot 1987). Approximately 80 years after its introduction, 93% of the yellow starthistle in Washington remained south of the Snake River (Roché and Roché 1988) within the *Agropyron/Festuca* zone (Daubenmire 1970). With increasing distance north from this zone, yellow starthistle invasion has been restricted to warmer sites. In northeastern Washington, yellow starthistle has been limited primarily to steep south-facing slopes of natural grasslands, in contrast to its wider distribution in southeastern Washington on gentle slopes and bottomlands (Talbot 1987). The critical factors at the northern limits of its ecologic amplitude appear to be short and longwave radiation during the winter, both of which are less limiting on steep south-facing slopes at north latitudes. These observations concur with reports that yellow starthistle did not persist in northern Europe, even following repeated introductions (Prodan 1930).

In the hotter, drier climate of southcentral Washington, yellow starthistle has invaded shrub steppe rangelands only where disturbance eliminated or severely reduced perennial vegetation or in topographic positions with deep soils that receive and store additional water (Talbot 1987).

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Optimal conditions in southeastern Washington natural grasslands, i.e., south-facing slopes and deep silt loam soils, indicated that dual requirements of light for winter growth and soil moisture for reproduction during the summer drought period may be the critical limiting factors for yellow starthistle.

The implications of these studies are that, on deeper soils and climatic conditions of eastern Washington, a stand of adapted perennial grass can limit yellow starthistle if it is managed to provide two conditions: 1) shade over the soil surface from fall through spring and 2) soil water depletion from late spring through summer. Shallow soils do not have the potential to support enough vegetation to shade yellow starthistle, but in the absence of summer precipitation, perennials deplete soil moisture before normal starthistle maturation, limiting its competitiveness.

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Ungulate-Forest Relationships in Olympic National Park: Retrospective Exclosure Studies

Abstract

Twenty-five ungulate exclosures were established in Olympic National Park (23) and Olympic National Forest (2) in the 1930's and 1950's. We gleaned information from the early studies and, where possible resampled vegetation within and adjoining exclosures from 1987-1990 to describe effects of ungulates on forest vegetation. Exclosures were established on low elevation (<350 m) ungulate ranges; 21 were located on river valley floors in the Sitka Spruce or Western Hemlock Forest Zones, 2 were on valley walls or other upland sites in the Western Hemlock and Silver Fir Zones, 2 were in clearcuts. We provide examples where ungulate herbivory influenced the composition, morphology, and standing crop of forest vegetation at all structural layers (i.e., herbaceous understory, shrubs, lower tree canopy, and overstory canopy). In communities initially dominated by grasses or grasslike plants on valley floors, exclusion of ungulates resulted in decreased cover of grasses and forbs (usually), decreased species richness of forbs, and sometimes increased height and abundance of ferns. Shrub size and density increased following exclusion, particularly salmonberry and huckleberry. Ungulates influenced the recruitment and morphology of vine maple. Ungulate effects on establishment of overstory species were variable; browsing appeared to affect recruitment of Pacific silver fir and western red cedar following clearcut logging, but effects on other species were unclear. The importance of ungulate herbivory in determining forest composition is discussed in relation to the scale of other processes.

Introduction

The importance of herbivores to ecosystem dynamics has been documented in studies of natural grazing systems (e.g., Crawley 1983, Naiman 1988, McNaughton *et al.* 1989, Frank and McNaughton 1992). In long-established ungulate systems such as the Serengeti, herbivores not only determine substantially the genetic and species composition of grassland vegetation, but herbivory may actually increase plant productivity by accelerating nutrient fluxes through the ecosystem (McNaughton 1985). Forest systems are less well understood, but moose (*Alces alces*) browsing is known to change the species composition, structure, nutrient availability, and long-term dynamics of boreal forests (Pastor *et al.* 1988, McInnes *et al.* 1992). These and other studies show that mammalian herbivores interact strongly with vegetation and are not just passive components of ecological systems. Early attempts to evaluate ungulate-forest relationships on the Olympic Peninsula began over 50 years ago when ungulate exclosures were constructed and periodically maintained. Only preliminary findings from these studies have been published (Schwartz and Mitchell 1945). We examine information assembled from 25 ungulate exclosures established in the 1930's and 1950's in Olympic National Park and Olympic National For-

est. Our goal was increased understanding of the long-term effects of native ungulates in forests in the Pacific Northwest. This work is part of a larger effort to understand the influence of ungulate herbivory on forest dynamics (Happe *et al.* 1990, Schreiner *et al.* submitted, Happe 1993, Woodward *et al.* 1993).

Although exclosures have been widely used to evaluate effects of wild and domestic ungulates and other mammals on plant communities, data derived from them may be difficult to interpret. Potential problems include small size and numbers, subjective placement of exclosures and associated sample plots, and modification of soil moisture and temperature regimes by the fences (Daubenmire 1940, Heady 1968, Houston 1982). Ungulates may be attracted to the fences, thus intensifying grazing or trail formation immediately outside. The intensity of herbivory may therefore be exaggerated when grazed plots are located too near the fence (Heady 1968). Moreover, it is risky to apply interpretations from a few exclosures to entire ungulate ranges because exclosures are small relative to ecological forces, such as fire, that drive vegetation dynamics over time (e.g. Mueggler and Bartos 1977).

We acknowledge these difficulties and others, such as the lack of statistical design, in the early studies on the Olympic Peninsula. Nevertheless, these exclosure studies span 55 years and provide an opportunity to evaluate long-term effects of

¹Current address: Cooperative Park Studies Unit, College of Forest Resources AR-10, University of Washington, Seattle, WA 98195

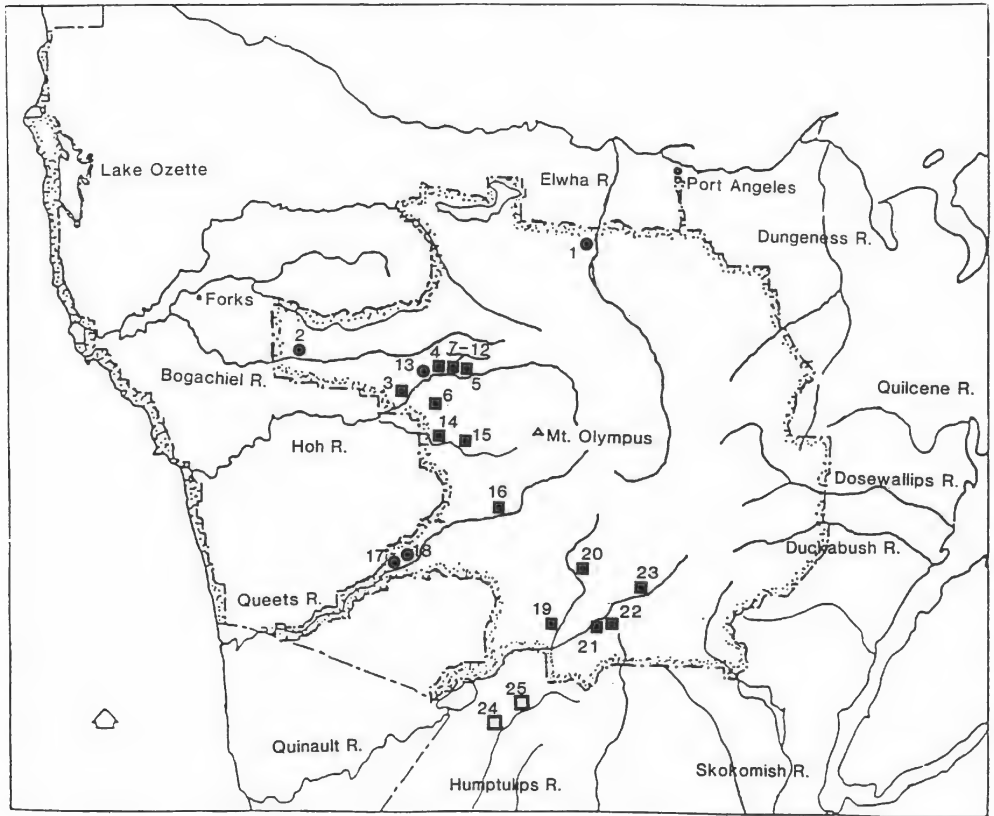


Figure 1. Approximate locations of 25 ungulate exclosures, Olympic Peninsula, Washington (Schwartz ■, Newman ●, and USFS □).

ungulates on the coniferous "rain" forest ecosystem unique to the Olympic Peninsula (Franklin and Dyrness 1988). Exclosures can provide insight into ecological processes if the information is interpreted carefully (e.g., Pastor *et al.* 1988, McInnes *et al.* 1992).

Study Area

Exclosures were established on low elevation (<350 m) ungulate ranges on the western half of Olympic National Park, Washington (Figure 1). The area has a maritime climate with relatively dry summers and wet winters. Annual precipitation ranges from 150 to 400 cm (NOAA 1978) with winter precipitation falling mostly as rain. Mean annual temperature at Forks is 10°C, with January as the coldest month (4°C) and July-August the warmest (16°C) (Phillips and Donaldson 1972).

Twenty-one exclosures were located on river valley floors in the Sitka spruce (*Picea sitchensis*) or Western Hemlock (*Tsuga heterophylla*) Zones (*sensu* Franklin and Dyrness 1988) where plant communities occur on river terraces of successively greater age (Fonda 1974). Valley floor forests have been described as a sere from pioneer red alder (*Alnus rubra*) on active floodplains, through black cottonwood (*Populus trichocarpa*)/Sitka spruce on younger terraces, to stands of western hemlock and Sitka spruce on older terraces (Fonda 1974). However, these successional patterns vary among river valleys depending on disturbance history (McKee *et al.* 1982). Three exclosures were located on valley walls in the western hemlock or Pacific silver fir (*Abies amabilis*) zones; one was in an old field.

Elk show two life history patterns in the study area: (1) year-round residence and (2) seasonal

migrations to high elevation summer ranges (Jenkins and Starkey 1982, Schroer 1987, Schroer *et al.* 1993). Elk densities on winter ranges in the park are approximately 6-7 elk/km² (Houston *et al.* 1987, 1988). Elk utilize certain vegetation types and landforms disproportionately. This produces a marked gradient in herbivory; use is concentrated on younger river terraces and floodplains, it is lower on older terraces, and least on the valley walls (Jenkins and Starkey 1982, 1984). Black-tailed deer (*Odocoileus hemionus*) occur throughout the area, but generally at lower densities. The elk:deer biomass ratio is estimated to be about 100:7 on west side river drainages (Leslie 1983). Ungulate predators include cougar (*Felix concolor*) and black bear (*Ursus americanus*).

Methods

Twenty-three exclosures were established in Olympic National Park during two periods when there was concern about elk-vegetation relationships: 1934-1936 (18 exclosures) and 1952-1958 (5). J. E. Schwartz constructed 12 permanently closed exclosures and two series of three "take-down" exclosures which could be left open for predetermined amounts of time. These exclosures were actually established on Olympic National Forest lands that became Olympic National Park in 1938. The second pulse of exclosure construction was by C. C. Newman, who also repaired and measured some of the Schwartz exclosures. In addition, two exclosures were established in 1957 in Olympic National Forest. Although our work focused on the park, exclosures in the national forest provided an opportunity to compare the effects of ungulate herbivory in managed forests. From 1987 to 1990 we gleaned information from the early studies and, wherever possible, resampled vegetation within and adjoining exclosures. The names and numbers used to identify exclosures changed over time which resulted in considerable confusion. Exclosures are numbered from north to south for our presentation (Table 1, Figure 1).

Schwartz Permanent Exclosures (Nos. 3-6, 14-16, 19-23)

J. E. Schwartz constructed 12 permanent exclosures from 1934 to 1936 in the Hoh, South Fork Hoh, Queets and Quinault river valleys. Two have never been relocated or sampled (Nos. 6, 20). The remaining 10 were either 0.09 ha (n=6) or

0.19 ha (n=4) and were constructed of split rails and barbed wire (n=8) or woven wire (n=2). Schwartz was concerned about the level of browsing on three species he considered "key browse species," salmonberry (*Rubus spectabilis*), vine maple (*Acer circinatum*), and huckleberry (*Vaccinium parvifolium*, and *V. alaskense*) (Schwartz 1939, Schwartz and Mitchell 1945, Schwartz pers. comm. 1990).

Schwartz described vegetation by estimating "density of ground cover" on a scale of 1-10 in one (sometimes two) 9.3 m² plots inside exclosures. Estimates included only herbaceous species and omitted mosses. On different 9.3 m² plots he charted aerial cover of shrubs and also estimated percent cover of "grass" (including sedges), and "weeds" (i.e., forbs including ferns). Unfortunately only preliminary data from seven exclosures remain (Schwartz and Mitchell 1945).

Schwartz Takedown Exclosures (Nos. 7-12)

Schwartz constructed six "takedown" exclosures in 1936 in addition to the permanent exclosures. These were designed to measure the effects of regulated browsing on vine maple (Nos. 7-9) and huckleberry (Nos. 10-12). The three exclosures forming each series were less than 50 meters from one another. The original objective was to allow wintering elk to browse shrubs to predetermined levels (25, 50, 75% utilization of annual production), close the exclosures and monitor shrub response (Schwartz 1939). All exclosures were opened in spring 1937 and closed permanently by 1938 (Schwartz 1990 pers. comm.). All data have been lost.

C. C. Newman (1953) repaired six of the Schwartz exclosures and sampled vegetation inside and outside four in 1952 and 1955. Percent cover was estimated as < 1% or as midpoints in 10 subsequent classes at 10% increments. Shrub stems were counted on 2.3 m² circular plots.

Newman Exclosures (Nos. 1, 2, 13, 17, 18)

Newman constructed five variously sized exclosures of woven wire from 1953 to 1958 (Table 1). Three were in Sitka spruce stands in different river valleys (Bogachiel, No. 2; Hoh, No. 13; Queets, No. 18), one in a red alder stand (Elwha, No. 1) and one along an old-field/vine maple ecotone (Queets, No. 17). Three exclosures were established at particularly heavily grazed sites (Nos. 1, 13, 17).

TABLE 1. Characteristics of 25 ungulate exclosures established in Olympic National Park and Olympic National Forest, 1934-1958.

Area/ID	Date Est. (Mo.)	Orig. Area Biol. ¹ (ha)	Veg. Type ²	YEARS SAMPLED AND METHODS USED ³																Comments
				35	40	45	50	55	60	65	70	75	80	85	90					
OLYMPIC NATIONAL PARK																				
<u>ELWHA RIVER</u>																				
1 Hughes Cr.	1956	(6)	N	0.03	ALD/SB (F,L)						BBBBBBBBBBB			B		D			Intact 1990	
<u>BOGACHIEL RIVER</u>																				
2 Mosquito Flat	1953	(?)	N	0.01	SPR/VM (F,L)						BBBBBBBBBBBBBB		P		B		D		Intact 1990	
<u>HOH RIVER</u>																				
3 Hoh No. 1 (Snider Cr.)	1934	(12)	S	0.19	HEM/VM,HB (F,U)	AP	A			BPPB		X					D			
4 Hoh No. 2 (Ranger Sta.)	1935	(10)	S	0.19	HEM/VM (F,L)	A	A			BP B*P							D			
5 Hoh No. 3 (Happy Four)	1935	(8)	S	0.19	?/VM,HB (F,U)	A	A													
6 Hoh No. 4 (Jackson Cr.)	1936	(?)	S	?	?/HB (W)															
7 Takedown No. 1 (Ranger Sta.)	1936	(?)	S	0.02	HEM/VM (F,L)												D			
8 Takedown No. 2 (Ranger Sta.)	1936	(?)	S	0.02	HEM/VM (F,L)															
9 Takedown No. 3 (Ranger Sta.)	1936	(?)	S	0.02	HEM/VM (F,L)					PB B							D			
10 Takedown No. 4 (Ranger Sta.)	1936	(?)	S	0.02	HEM/HB (F,U)												D			
11 Takedown No. 5 (Ranger Sta.)	1936	(?)	S	0.02	HEM/HB (F,U)												D			
12 Takedown No. 6 (Ranger Sta.)	1936	(?)	S	0.02	HEM/HB (F,U)												D			
13 Hall of Mosses	1953	(7)	N	0.02	OPEN/SB (F,U)					BBBBBBBBBBBBBB	X						D		Spaded, 1953	
<u>SOUTH FORK HOH RIVER</u>																				
14 Hoh No. 5 (Big Flat)	1935	(11)	S	0.09	SPR/HB (F,?)					BPB				X	P		D			
15 Hoh No. 6 (Section 10)	1936	(?)	S	0.09	HEM/HB (F,?)												D			
<u>QUEETS RIVER</u>																				
16 Queets No. 2 (Pelton Cr.)	1935	(10)	S	0.09	HEM/HB (F,?)		P			PP P				PP		X				
17 Andrews Field	1953	(?)	N	0.01	OPEN/VM, GRASS (F,L)					BBBBBBBBBBBBBB						BX	D		Old field	
18 Big Fir	1958	(4)	N	0.04	HEM/HB/ (F,U)					BBBBBBBBB						BX	D			
<u>Quinault River</u>																				
19 Quin. No. 1 (Irely Trail)	1935	(8)	S	0.19	SPR/VM (F,L)	A	A			X							D			
20 Quin. No. 2 (Wildrose Cr.)	1935	(9)	S	0.09	HEM/HB (F,?)	AP	A													
21 Quin. No. 3 (East Fork)	1935	(8)	S	0.09	SPR/VM (F,L)	A	A			B B							D			

TABLE 1. Continued.

Area/ID	Date Est. (Mo.)	Orig. Area Biol. ¹ (ha)	Veg. Type ²	YEARS SAMPLED AND METHODS USED ³																Comments
				35	40	45	50	55	60	65	70	75	80	85	90					
22 Quin. No. 4 (Graves Cr.)	1935 (?)	S	0.09 BLM/VM,SB (F,L)	A	A	P			P											D
23 Quin. No. 5 (Fire Cr.)	1936 (?)	S	0.09 SILF/HB (W)						P											D

¹ N= C. Newman; S= J. Schwartz; F= U.S. Forest Service.

² Major overstory tree/shrub (ALD= red alder, BLM= bigleaf maple, HEM= western hemlock, SILF= Pacific silver fir, SPR= Sitka spruce, HB= huckleberry, SB= salmonberry, VM= vine maple) and location (W= valley wall, F= valley floor, Upper (U) and Lower (L) terraces.

³ Measurements include:

A= Cover in 9.3 m² plots, B= Cover & stem count in 2.3 m² plots, C= tree mortality and growth, D= Examination and/or measurements, this study, P= photo.

Photos taken the same year as measurements are not indicated, X= Known to be no longer functional.

⁴ Also cover and sociability, Sharpe 1956.

Apparently, No. 17 was to evaluate the ability of vine maple to recolonize an abandoned hayfield in the absence of browsing. No. 13 was built mainly to determine if vine maple and bigleaf maple require mineral soil to reproduce from seed; one half of the enclosure and a corresponding outside plot were spaded in 1953.

Percent cover by species was estimated on eight (four inside, four outside) 2.3 m² circular plots. Plots were established systematically, one in each quarter of the enclosure with a similar pattern (usually) outside. Data were collected by park personnel regularly through 1965 and again in 1982, although methods and seasons varied.

Olympic National Forest Enclosures (Nos. 24,25)

Two 0.8 ha enclosures made of woven wire were established in 1957 on clearcut western hemlock/Pacific silver fir stands logged in 1955; both were essentially intact in 1990. Logging slash was left unburned at No. 24 and burned at No. 25. One-half of each enclosure was planted with 2-year old Douglas-fir (*Pseudotsuga menziesii*) seedlings and the other half was allowed to regenerate naturally. Mortality and growth rates were measured from 1957 to 1962 on 100 planted Douglas-fir seedlings inside and outside each enclosure (Harrison 1963). Species composition and cover of shrubs, grasses and forbs were measured inside No. 24 during 1957 (Brent 1957).

Recent Samples

Schwartz Permanent Enclosures. We examined eight enclosures from 1986-1990; none was intact. Tree composition was sampled in six ex-

closures (Nos. 3, 14, 19, 21, 22, 23) using one or two 100-400 m² plots inside and outside (the two remaining sites had been altered by extensive treefall and were not sampled). Cover of large organic debris (LOD) was estimated and tree age was obtained for all individuals in each plot, either from increment cores taken close to the ground or basal sections of saplings 1-4 cm in diameter. Overstory cover was estimated overall and for each species to the nearest 10 percent. Inside and outside plots were comparable with respect to overstory composition and cover of LOD. Plots inside enclosures were placed a minimum of 2 m from fencelines, while outside plots were at least 10 m and usually much further from fencelines. Quinault River enclosures (Nos. 19-23) were sampled by Pfister and Pfister (1989) under our direction. Sampling focused on vine maple age and morphology in No. 4 (see takedown enclosures).

Schwartz Takedown Enclosures. We relocated the six takedown enclosures in 1990. While examining the vine maple series, we noticed that apically dominant stems originated either directly from the ground or from branches of older stems, and stem orientation varied from vertical to horizontal. Therefore, we measured age, stem length (rather than height above ground), number, diameter, and morphology (originating from branch or ground rooted) of stems > 1 cm. Samples were taken inside Nos. 7 and 9; we also included No. 4 (permanent) because vine maple density was comparable. Takedown No. 8 was not sampled because vine maple was sparse. Plot sizes ranged from 9.5 x 14.3 m to 20 x 20 m for a total area of 675 m² inside and 850 m² outside. Because enclosures were placed specifically around clumps of vine maple, we deliberately established outside

plots in stands having comparable composition and stem density.

We measured dimensions of huckleberry clumps (stems arising from a common root crown) in 8.5 x 14 m plots inside and outside Nos. 11 and 12. Exclosure 10 was omitted because huckleberry was uncommon. Outside plots were chosen which had huckleberry-dominated shrub layers, and overstory types, slopes, aspects and geomorphic surfaces similar to the exclosures. We counted the number of stems and measured height of the tallest stem, length and width of each clump. Canopy area was computed as an ellipse from the length and width. Several of the largest stems at each site were cut for determining age.

Newman Exclosures. We examined all five Newman sites from 1987-1990; two exclosures were intact (Nos. 1 and 2). We measured cover of shrubs (1 x 4 m plots) and herbaceous species (1 x 1 m plots) in classes of <1, 1-5, 6-25, 26-50, 51-75, 76-95, and 96-100%. Fourteen subplots were placed in a single 8 x 20 m macro plot inside exclosures and distributed seven each in two 8 x 20 m macro plots outside. As with the Schwartz exclosures, cover of LOD was measured, and ages of all trees >1 cm in diameter at the base were determined from cores or basal disks.

Olympic National Forest Exclosures. We sampled species composition, age and growth (i.e., dbh and height) of trees on two (burned, No. 25) or three (unburned, No. 24) 225 m² plots inside and out of each exclosure. We sampled the unplanted site at No. 25 and the planted site at No. 24. We avoided sampling other sites because vegetation heterogeneity prevented us from locating paired plots in and out of exclosures.

Photographs. In addition to sampling vegetation, we examined historic photographs. We located 48 photos of Schwartz exclosures from construction through 1980, 349 photos or slides of Newman exclosures, and 2 photos of the Forest Service exclosures.

Analysis, interpretation, and presentation of data from all four groups of exclosures posed certain difficulties. Although the total number of exclosures is large, only four vegetation types were replicated (see Table 1). Within these groups, some exclosures were not found, or appeared to be atypical for reasons other than herbivory, or included too few individuals (particularly trees) to provide meaningful conclusions. Therefore, our presenta-

tion is mostly narrative and focuses on replicated comparisons; statistical treatments are limited to robust tests with the fewest underlying assumptions. Percentage data was transformed by the arcsine of the square root before analysis. Interpretations from measurements were also compared to the photos.

Results

We believe that all exclosures were initially effective in excluding elk and deer. Fences were generally at least 2.5 m high with construction which appeared to preclude ungulates, but not smaller herbivores such as snowshoe hares (*Lepus americanus*) and rodents. We do not know how long some exclosures were effective (Table 1). Several of the Schwartz exclosures were in disrepair by the early 1950's (Newman 1953), but some were enough intact that Newman considered repairs worthwhile.

Herbaceous Understory

Results from the Schwartz exclosures showed that understory vegetation responded quickly, and changes persisted for at least 21 years (Table 2). Specifically, grass cover decreased and ferns tended to increase. Similarly, grass cover decreased with time inside four of five Newman exclosures while forbs and ferns generally showed parallel changes in and out (Table 3).

Data from Newman exclosures were recorded by species, providing information about changes in species richness of forbs. During the first three years of measurements at No. 1 on the Elwha, five to eight species were encountered inside and five to seven outside. After 31 years, youth-on-age (*Tolmiea menziesii*) completely dominated the herbaceous layer inside, while eight species of forbs occurred in outside plots. At the other four sites, data collected until 1965 showed that cover of clover (*Trifolium* spp.) (Nos. 2, 13, 17), liverworts (No. 2), buttercup (*Ranunculus repens*) (Nos. 2, 17) and dandelion (*Taraxacum officinale* and/or perhaps *Hypochaeris radicata*) (No. 17) declined inside exclosures but persisted outside. Oregon oxalis (*Oxalis oregana*) (No. 18), dock (*Rumex* spp.) (No. 13), and chickweed (*Stellaria* spp.) (No. 1) had similar cover in and out of exclosures. Thus, species richness of forbs outside exclosures was greater than or equal to richness inside and total cover of forbs tended to be greater outside exclosures by 1987.

TABLE 2. Summary of vegetation cover changes for Schwartz and Newman exclosures at several post-establishment time intervals. Symbols indicate change in vegetation category. Comparisons are between vegetation inside exclosures and inside at an earlier date (Schwartz, 3 year interval), or with outside (all others). Data are from Schwartz and Mitchell (1939), Newman (1953, 1955), and Sharpe (1956).

Exclosure	Intervals (years)	Change in Vegetation Cover ¹			
		Grasses	Forbs	Ferns	Shrubs
Coniferous Forest (Schwartz ²)					
No. 3	3, 17, 20	—	0	?	+
No. 4	3, 17, 20, 21	—	0	+	+
No. 5	3	—	+	?	+
No. 9	17, 20	0	0	0	+
No. 14	17, 20	0	0	+	+
No. 18	2-4	?	0	0	0
No. 19	3	—	—	?	+
No. 20	3	?	—	?	+
No. 21	3	—	—	?	+
Coniferous Forest (Newman)					
No. 2	2-7, 9, 10, 12	—	0	0	+
No. 13	3-5, 7-9, 12	—	?	+	+
Alder Flat (Newman)					
No. 1	1-3, 5, 6, 8, 9	—	0	?	?
Bigleaf Maple (Newman)					
No. 22	3, 17	—	—	0	+
Old Field (Newman)					
No. 17	2-4, 5, 7-9	—	0	?	?

¹Key: (—) = less inside at every interval, (+) = more inside at every interval, (0) = no difference or contradictory changes with interval, (?) = category was not reported.

²Decrease in grass cover and increase in shrub cover inside exclosures was significant over 3-year interval for Schwartz exclosures ($p < 0.05$, sign tests); grass cover was significantly less and shrub cover was significantly greater inside versus outside at 17-year interval ($p < 0.05$, sign tests).

TABLE 3. Dimensions of huckleberry clumps in Schwartz take-down exclosures Nos. 11 and 12 and control plots.

		Distribution			Clump Dimensions		
		Clump Density (no./m ²)	Stem Density (no./m ²)	Canopy Area (area/m ²)	Height (cm)	Canopy Area (m ² /m ²)	Stems (no.)
In	No. 11	0.51	6.2	0.24	56.1	0.41	10.6
	No. 12	0.58	5.4	0.50	94.1	0.86	9.3
	Mean	0.54	5.8	0.37	75.1	0.64	10.0
Out	No. 11	0.47	2.0	0.14	62.8	0.31	4.0
	No. 12	0.54	3.0	0.22	69.6	0.41	6.0
	Mean	0.50	2.5	0.18	66.2	0.36	5.0

Photographs generally corroborated measurements. The most striking changes in vegetation occurred following ungulate exclusion from plant communities where understories were dominated initially by grasses or grass-like plants, as opposed to moss and swordfern dominated sites (compare Figures 2 and 3). These relationships held in both conifer forests and alder stands, represented in both Schwartz and Newman exclosures.

Shrubs

Shrub species, particularly salmonberry and huckleberry, increased inside both the Schwartz and Newman exclosures (Tables 2 and 3). This occurred in all forest types and was supported by the photographs.

Our measurements focused on huckleberry at Nos. 11 and 12. Huckleberries produce multiple stems from a single root mass, and each clump seemed to represent an individual plant. Fifty-four years post-establishment, clump density was similar inside and out, however canopy dimensions and numbers of individual stems were greater inside (Table 4). Canopy area inside was greater by a factor of nearly two. Effects persisted even after the exclosures had collapsed because ungulates rarely consumed thick, woody stems. The largest stem we found had 4 cm basal diameter and was 32 years old.

Lower Tree Canopy

Nearly all vine maple individuals established both in and out of exclosures since construction in 1936 (Figure 4). However, mode of establishment and morphology was affected by ungulates. Ground-rooted individuals (established from seed or lateral root buds) predominated inside exclosures, while branches that achieved apical dominance after the main trunk had fallen were the source of new individuals outside (Figure 4).

Age and stem length of cohorts were compared inside and out of exclosures (Figure 5). The majority of young stems outside tended to be shorter than 2 m, while many stems inside were longer than 2 m (Figure 5a). Stem length of 15 to 29-year-old trees showed similar bell-shaped distributions both inside and out (Figure 5b). Finally, cohorts older than 29 years outside fell predominantly into two stem classes and were rarely longer than 8 m (Figure 5c).

Overstory

We saw relatively few consistent effects of herbivory on overstory composition in Schwartz and Newman exclosures. They were simply too small to contain enough individuals to give conclusive results. The only replicated results came from Nos. 3 and 18 with hemlock overstories and significant LOD inside (22%, 38%) and out (16%, 38%). More western hemlock established inside Nos. 3 (22 stems) and 18 (19 stems) compared with outside (No. 3, 14 stems; No. 18, 4 stems) following exclosure construction. In contrast, more Sitka spruce established outside (No. 3, 15 stems; No. 18, 5 stems) than in (No. 3, 2 stems; No. 18, 0 stems).

Results from the Olympic National Forest exclosures showed that total density (living and dead) and density of stems living after 33 years were greater inside exclosures for Pacific silver fir and western red cedar (Table 5). Density of living Douglas-fir did not differ in and out of No. 24, but there were more dead stems outside. We did not sample the planted portion of No. 25.

Discussion

Utility of Exclosure Studies

Although these early exclosures provide insight into the effects of herbivory, subsequent ungulate biologists would likely consider them to be too small (e.g., Heady 1968), because fences of small exclosures may alter microclimate and grazing intensity. We do not know the proximity of fences to most plots used to sample vegetation in the original studies. However, several surviving sample points outside Nos. 1, 3, and 22 were within a few meters of the fence, possibly exaggerating levels of herbivory sampled by Schwartz and Newman. The rugged construction of exclosures may have interfered with normal air currents and provided additional shade; they may have harbored a larger than normal snowshoe hare population (Sharpe 1956). Taller plants seen along fencelines today may be explained by greater light interception and/or by reduced competition from grazed plants outside fencelines. Also, vegetation contrasts may have been exaggerated in the Schwartz exclosures because they were located on heavily grazed sites.

These caveats granted, we believe the primary influence on vegetation change was the exclusion of ungulates. Our results may reflect ungulate



1958



1962

Figure 2. Inside No. 18 along the Queets River several months and four years post-establishment. Note that comparatively little change in composition or standing crop has occurred in the moss (*Hylecomium splendens*) and oxalis dominated plant community on this upper terrace.



1955

Figure 3. Number 13 on the Hoh River at 2 years, 6 years, and 12 years post-establishment. Note increased standing crop of grasses initially, which were displaced by salmonberry. A grass-dominated community with scattered ferns persists outside. Note the decomposition of the log at left background and the growth rate of the spruce.



1959



1965

TABLE 4. Comparison of establishment and survival of Pacific silver fir, western red cedar and western hemlock in and out of two exclosures established in clearcuts. Slash was burned in one clearcut (No. 25) and left in the other (No. 24). Douglas-fir was sampled only at No. 24. Results are the mean of two plots (No. 25) or three plots (No. 24) in and out of exclosures.

		Stems/ha					
		Living		Dead		Total	
		In	Out	In	Out	In	Out
P. Silver Fir	No. 24	104	15	0	59	104	74
	No. 25	156	44	155	22	311	66
W. Red Cedar	No. 24	104	0	15	0	119	0
	No. 25	289	44	266	67	555	111
W. Hemlock	No. 24	888	889	341	1081	1229	1970
	No. 25	1778	1311	2178	644	3956	1955
Douglas-fir	No. 24	326	340	15	104	341	444

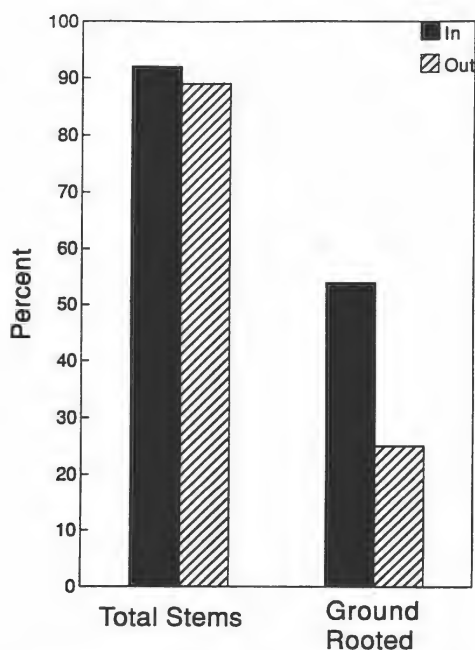


Figure 4. Establishment of vine maple since exclosure construction in 1936. Nearly all stems in and out of exclosures have established since 1936 (left), while a higher percentage (at $p = 0.060$) of stems inside exclosures are ground-rooted (right).

herbivory at the high end of the grazing intensity gradient described earlier, because a high level of grazing was prerequisite for siting many exclosures (Schwartz 1990 pers. com.). Of 22 exclosures

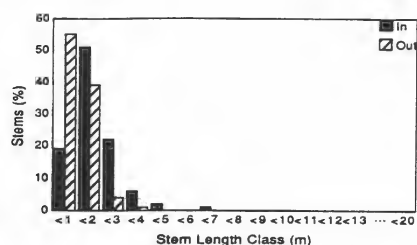
examined by us in the park, only one was on a valley wall, seven were on "upper terraces," ten were on "lower" terraces and four were on valley floor sites where terrace level could not be determined.

Effects of Ungulates on Vegetation

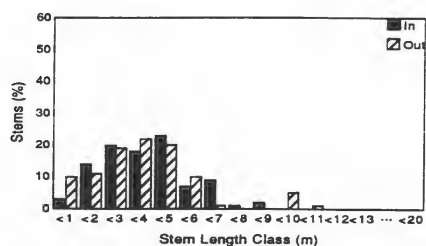
Understory. The greatest changes in herbaceous understory vegetation resulting from exclusion of ungulates occurred in communities initially dominated by grasses or grass-like plants. Specifically, grass cover decreased, abundance and height of ferns usually increased, species richness of forbs decreased, and forb cover usually decreased. Because the decrease in grass cover was not necessarily linked to an increase in forb cover, ungulates apparently did not mediate a direct competitive relationship between grasses and forbs. Forb species that declined in the absence of ungulates included clover, buttercup, and dandelion—a response possibly explained by trampling tolerance and greater light requirements. In contrast, youth-on-age thrived in the absence of grazing at No. 1, perhaps reflecting shade tolerance. Moreover, because clover, buttercup, and dandelion are introduced species, our results support the hypothesis that most introduced plants may become less abundant in the absence of disturbance (Harper 1977).

Shrubs. In the absence of ungulates, shrub size and stem density increased, particularly salmonberry and huckleberry, with possible effects on other layers. The consequent increase in shade is an additional environmental modification due to

a) 5-14 Years



b) 15-29 Years



c) 30-54 Years

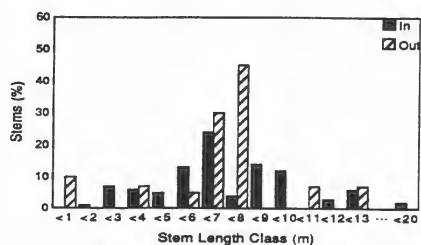


Figure 5. Distribution of stem length classes for three age cohorts of vine maple at Nos. 4, 7, and 9 (combined), measured 54 years post-establishment. Comparison is made between stems growing inside and outside exclosures.

herbivory experienced by the herbaceous layer. Competition with shrubs has been used by others to explain reduced Douglas-fir regeneration inside exclosures compared with out (Hanley and Taber 1980).

Lower Tree Canopy. Vine maple is consumed by both elk and deer (Leslie *et al.* 1984). In spite of its ability to grow beyond the reach of ungulates, its life history does not allow it to avoid herbivory. Commonly, the flexible trunks bend to the ground (Anderson 1969), which makes foliage and twigs available to ungulates. In addition, basal sprouts are browsed. Their persistence in the presence of

ungulates may be at the expense of stem length growth. Stems were longer and distributed in more stem length classes in the absence of ungulates. In addition, we suspect that ungulates limited establishment of vine maple from seeds or by lateral root buds, thus encouraging a clumped distribution.

Overstory. The ability of ungulates to influence the eventual composition of the overstory (by differentially affecting species recruitment) could not be determined. Ungulates seemed to influence recruitment under certain circumstances. In valley floor sites where large organic debris (LOD) was present and western hemlock dominated the overstory, elk may have impaired establishment of hemlock in favor of Sitka spruce. Ungulates inhibited establishment of western redcedar and Pacific silver fir in Olympic National Forest clearcuts surrounded by mature forests during the 1950's. Our results showing greater mortality of planted Douglas-fir outside No. 24 contrasts with those of Hanley and Taber (1980) showing greater mortality of planted Douglas-fir inside exclosures.

The effect of ungulate herbivory in these forests is complex and the intensity of herbivory varies considerably in time and space. Our varied results, particularly with reference to western hemlock establishment, illustrate these points. Additionally, results from sampling tree age distributions (Harmon and Franklin 1983) did not support the hypothesis that western hemlock saplings on the South Fork Hoh River became established when elk densities were low (due to over hunting at the turn of the century). However, more recent observations of two intact 0.5-ha exclosures established in 1980 on the South Fork Hoh River show that elk do hinder hemlock establishment (Harmon pers. comm., Schreiner, pers. obs.). These contrasting results suggest that ungulate effects on tree establishment vary temporally and spatially.

These exclosures generally represent examples of fairly intense herbivory. Elk subpopulations may have just passed through an eruptive overshoot (Jenkins 1981) when the first exclosures were established in the 1930's (Woodward *et al.* 1993). Thus, levels of herbivory measured initially may have been more intense than subsequent levels. By the late 1950's, Newman (1958) considered that elk and vegetation had reached acceptable equilibria in the park, the current view as well (Jenkins 1981, Schreiner *et al.* submitted). We believe these exclosures illustrate the general nature

of ungulate herbivory in western Olympic Peninsula forests, although the intensity of effects change with ungulate density.

Ungulates and Forest Dynamics

Forest processes operate at a variety of scales, some which can be influenced by ungulate herbivory and some which cannot. Formation of canopy openings (i.e., gaps; see Platt and Strong 1989) is an important process influencing forest composition at various time intervals and at both fine- and coarse-grained spatial scales. Fine-grained gaps are created by insect, root pathogen, and wind induced mortality of one to a few trees (Spies and Franklin 1989). These small gaps are produced so frequently that differential establishment of various tree species in them may change the composition of the canopy over time. The exclosure studies reflect the effects of herbivory at these fine-grained, relatively short duration scales. At such scales, ungulates seem capable of influencing the direction and rate of plant succession.

However, chronic disturbances operating at small spatial scales over short time frames are overridden by larger, landscape-scale disturbances.

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- The longer term dynamics of unmanaged forests on the western Olympic Peninsula appear to be driven by infrequent large-scale disturbances, such as fires (Agee 1993), floods (Fonda 1974), or catastrophic windthrow (Henderson *et al.* 1989). While ungulate herbivory may indeed affect forest regeneration at the scale of individual tree gaps, their influence following large, catastrophic disturbances seems inconsequential by comparison. Our results support the general conclusion that the extent to which herbivores can cause changes in forest ecosystem processes may depend on the scales of other disturbances (Pastor *et al.* 1988).

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**ABSTRACTS OF THE
NORTHWEST SCIENTIFIC ASSOCIATION
67th ANNUAL MEETING**

Held in Conjunction with:

The Society for Northwestern Vertebrate Biology

The Association of Washington Geographers

*The American Society of Photogrammetry
and Remote Sensing, Puget Sound Region*

The Northwest Lichen Guild

and

The Rare Plant Consortium



**March 23-26, 1994
Central Washington University
Ellensburg, Washington**

SPATIAL DISTRIBUTIONS OF TWO GENTIANAS IN ASSOCIATION WITH AN ILL-DEFINED SUBALPINE WETLAND BOUNDARY IN SHEEP-GRAZED AREAS OF HORSESHOE BASIN, WA. A.B. Adams, ECO-DAD, Whistler, B. C. and Bill Crooks, University of Guelph, Ontario.

GIS analysis with an enhancement filter routine was used with raster data to classify subalpine wetland habitats in an investigation of boundary integrities. Some boundaries are well-defined, others ill-defined. The ill-defined areas corresponded with tundra-like hummocky meadows. Gentiana glauca occurs in these meadows. GIS analysis of a second site where G. tenella grows in proximity with G. glauca showed that the former taxa did not occur on the hummocks. Lakes in the Pasayten are protected from sheep grazing with buffers, but not wetlands. This policy is limited in terms sensitive species protection and water retention capacity. We propose that grid analysis may be more suitable delineation method for some wetlands (vs. vector) in terms of cost and analysis, suggest that new methods of defining sympatric populations be developed based on scale of sampling, and provide information on the impact of grazing on subalpine ecosystem integrity and biodiversity.

THE LENGTH OF LARVAL LIFE IN COASTAL POPULATIONS OF THE TAILED FROG. Michael J. Adams, University of Washington, Seattle. R. Bruce Bury, National Biological Survey, Corvallis, Oregon.

The length of larval life for the tailed frog is reported as two to four years. We examined this trait at five coastal sites in the Oregon Coast Range and one in the Olympic Mountains, Washington. Total length and hind-leg length of tadpoles separated age-classes. Also, multiple samples within years clarified differences. Mid-summer samples revealed a high level of variation in developmental stage at the three southernmost sites, but all had a one-year larval period. The northern sites had two-year larval periods. Coastal populations were previously reported to have two-year larval periods. A one-year larval period may be possible in the southern Coast Range because of the mild climate and extended growing season (i.e., freezing temperatures are rare).

INSECT HAZARDS, WITH SPECIAL EMPHASIS ON YELLOWJACKETS. Roger D. Akre, Dept. Entomology, Washington State University, Pullman.

Various arthropods can pose hazards to researchers of vertebrates. These potentially harmful animals include poisonous spiders, bugs, bees, and yellowjackets. The latter are especially troublesome for people working in forested situations. Colonies can contain up to >5,000 workers, and stings from a disturbed colony can be extremely unnerving or even life threatening. All researchers in back country locations should carry an emergency medical kit.

VEGETATIONAL ANALYSIS OF AN UPLAND-WETLAND GRADIENT AT CANNERY POND, ANACORTES, WASHINGTON. Lori Allison, Western Washington University, Bellingham.

Gaps are defined as breaks in a forest canopy. Cannery Pond in Anacortes, Washington was an excellent site on which to test the hypothesis that a wetland functions as a gap in a terrestrial forest community. Forest and wetland gradients were analyzed along one continuous transect across the shoreline. Three zones were recognized along the transect: an upland Abies grandis/Polystichum munitum community, a seral shoreline Alnus rubra/Rubus ursinus community, and the wetland Typha latifolia/Lemna minor community. Solar radiation, wind, soil moisture, and soil organic matter increased significantly from the upland toward the wetland. The changes in environmental factors paralleled the shifts in vegetation.

PRELIMINARY ASSESSMENT OF THE STATUS OF THE NORTHERN LEOPARD FROG IN WASHINGTON STATE. Sandy J. Andelman, Washington Natural Heritage Program, Olympia. Kelly McAllister, Washington Department of Wildlife, Olympia.

The northern leopard frog has declined throughout considerable portions of its range. Since systematic surveys had not been carried out for this species in Washington for 40 years, we compiled information on their historic distribution in Washington. From March through October, 1993, historic sites were visited and time-constrained searches for leopard frogs were conducted. Leopard frogs were found at only one site, and the reproductive status of that population remains unclear. An additional report from a site in Whitman County also has been received. The results of these preliminary surveys suggest that the northern leopard frog may be extirpated from 90% of its historic range in Washington. The causes of the decline remain to be determined, however, habitat loss has played a role, particularly along the Columbia River. Pesticides, as well as predation by exotic fish and/or amphibians, are other potential factors. Currently the northern leopard frog is not protected in Washington, and both of the known sites are vulnerable. Additional systematic survey efforts are needed during the coming year. In the interim, protection measures should also be implemented without delay.

DISTRIBUTION AND HABITAT SELECTION BY WINTERING TRUMPETER SWANS (*CYGNUS BUCCINATOR*) IN THE LOWER SKAGIT VALLEY, WASHINGTON. Paul S. Anderson, Seattle Water Department, Cedar Falls, Washington.

Weekly swan surveys were conducted by automobile between November and April 1990/91 and 1991/92 in the Skagit Valley, Washington. ARC/INFO was used to produce swan and crop distribution maps. Twenty-three surveys were completed in each study year. There were no major changes in swan geographic distribution during the winter. The temporal pattern of crop use was the same both years; corn in early winter, potatoes in mid winter, and potatoes and grass (pasture or winter wheat) in late winter. Potato fields received the highest swan use in 1990/91 (4098 swans) and 1991/92 (4287 swans). Of 11,885 ha of corn, pasture, potato, carrot, and winter wheat available to swans in 1991/92, swans were seen on 2860 ha, 24%. However, 451 ha (3.8%) accounted for 67% of swan use. There appears to be adequate Skagit Valley habitat to accommodate higher numbers of wintering swans.

LANDSCAPE- AND STAND-LEVEL STUDIES OF PILEATED WOODPECKERS: DESIGN CONSTRAINTS AND STAND-LEVEL RESULTS. Keith B. Aubry and Catherine M. Raley, USDA Forest Service, Pacific Northwest Research Station, Olympia, Washington

To study landscape-level habitat relationships of pileated woodpeckers, we began with a design consisting of adjacent managed and unmanaged landscapes in which environmental and ecological conditions were comparable. However, differences in accessibility and bird detectability between the study areas precluded equal sampling. These problems eventually forced us to abandon a paired design and focus instead on habitat use in the managed landscape. To estimate the availability of snags and decadent live trees for nest and roost sites within our 8,289 ha study area, we established 254 0.4 ha sampling plots. In each plot, we measured all snags and decadent trees ≥ 20 cm dbh and ≥ 1 m tall. To determine use by pileated woodpeckers, we located nest trees using call surveys and ground searches, and roost trees using radio-telemetry. We found 16 nest trees: 13 in western hemlock (6 snags and 7 decadent trees) and 3 in Pacific silver fir snags. We located 73 roost trees: 38 in western hemlock (31 snags, 6 decadent trees, and 1 live tree), 31 in western redcedar (12 snags and 19 decadent trees), and 4 in Pacific silver fir (3 snags and 1 live tree).

PCR AMPLIFICATION OF RESISTANCE GENES FROM POLLUTED SOILS. Matthew Awbrey and Donald Lightfoot, Eastern Washington University, Cheney.

The "Polymerase Chain Reaction" (PCR) allows for the amplification of a specific DNA sequences from as little as a single copy of template. This process can be used to isolate, amplify, and identify specific sequences which exist in relatively low numbers. We are attempting to use the PCR process on soil samples taken from areas polluted with heavy metals such as mercury and/or cadmium. Environmental and microbial studies have demonstrated the ability of some bacteria to resist the toxicity of these heavy metals, and the sequences of the resistance genes to mercury and cadmium have largely been determined. We have established a DNA extraction and purification protocol that has allowed us to isolate and amplify conserved regions of the bacterial 16S ribosomal RNA gene from soil samples. Affinity removal of humic acids coupled with gel electrophoresis have allowed semi-quantitative observation of 400 to 1200bp amplicons. These methods will be used to detect specific bacterial heavy metal resistance genes present in environmental samples. Due to the difficulties associated with extraction of genetic information from soil, this relatively simple, time-efficient method offers benefit to future bioremediation and micro/ecological studies.

GENETIC DIVERSITY AND GENE FLOW IN *MIRABILIS MACFARLANEI*. Jennifer L. Barnes and Paul G. Wolf, Utah State University, Logan.

The rare plant, *Mirabilis macfarlanei*, is restricted to 18 isolated populations along the Imnaha, Snake and Salmon Rivers in Idaho and Oregon. Genetic drift and inbreeding in small, isolated populations can result in low genetic diversity. However, gene flow can potentially overcome these effects. Enzyme electrophoresis was used to estimate levels of gene flow and genetic diversity for seven populations of *M. macfarlanei*. Measures of genetic diversity for *M. macfarlanei* were lower than for plants with similar life histories. Gene flow was compared among populations that ranged from 0.5 km to 22 km apart. The greatest level of gene flow occurred between populations that were 0.5 km apart, ($N_m=18$; where N_m is the number of individuals migrating per generation). Levels of gene flow decreased as distances between populations increased. The results indicate that isolated populations may require special protection because of reduced gene flow which may result in lower genetic diversity.

MOVEMENT OF RAINBOW TROUT IN THE UPPER YAKIMA RIVER BASIN. Eric L. Bartrand, Todd N. Pearsons and Steven W. Martin, Washington Department of Wildlife, Ellensburg.

Understanding the direction, distance, and timing of fish movement within or between populations can help determine the spatial scale and intensity of sampling necessary for monitoring. We tagged 7,235 rainbow trout (*Oncorhynchus mykiss*) larger than 174 mm FL with numbered external tags over a four-year period to determine patterns of movement. Fishes were collected for tagging by electrofishing and trapping and subsequently recaptured by electrofishing, trapping, and angling. Movements were determined by comparing their location of capture with the location where they were recaptured. During the four year study, mainstem fish movements ranged from 0 to 81.9 km with the majority moving less than 5 km. The distance moved was related to time of year and capture location. Average movement of fish tagged in the upper sections of the mainstem was significantly greater than those tagged in lower sections. The greatest average movement was in the spring, concurrent with the time of spawning. We suggest that a fish population monitoring plan should encompass the normal areal range of fish movement and sampling should be conducted when average fish movement is the least.

SILVICULTURAL CONTROL OF FOREST CANOPIES. Dean Rae Berg, University of Washington, Seattle.

Silviculturists agree that control of individual tree canopy, or the live crown, influences the quality and quantity of wood. Crown management is well known (e.g., juvenile spacing, thinning, pruning) but rarely referred to as canopy control. Unknown elements of silviculture include impacts on ecosystem level functions of the forest, in particular the forest canopy. There are also many questions about the scale and methods of control. Commonly used silvicultural variables are used to demonstrate canopy control processes. Forest resource management is in a constant state of revising methods. This view is summarized in three points; Performance criteria, Feedback, and Controllability. Updating and adapting management to either better meet stated goals or modify expectations is a continuous process. Forest management in this context becomes a powerful research tool that provides useful results in a timely manner.

POST FIRE REGENERATION AND CLONAL GROWTH STRATEGIES OF TWO FLORIDA SCRUB OAKS. Dawn M. Berry, University of Washington, Seattle., Eric S. Menges, Archbold Biological Station, Lake Placid, FL.

Small, isolated fragments of oak scrub survive undeveloped on Florida's xeric central ridges. One management objective for scrub preserves is to maintain various stages of development within each fragment so that species (including 20+endemics) with special habitat requirements will not be eliminated. We studied the clonal growth and resource allocation strategies of the two dominant scrub plants, *Quercus inopina* (Inopina oak) and *Q. geminata* (Sand-live oak) in order to understand and predict the effects of different fire regimes on them. Our results suggest that *Q. geminata* may be better able to persist in long-unburned, lower light environments because it's stems can live longer and its rhizomes can search for patches of light more efficiently than those of *Q. inopina*. Preliminary results from our studies of post-fire stem demography and below-ground storage dynamics suggest that both species grow rapidly during their first two post-fire growing seasons. In subsequent seasons, however, *Q. inopina* growth slows as its resource allocation shifts to below-ground storage while large *Q. geminata* stems continue to grow rapidly. These results suggest that *Q. geminata* will be favored by long fire return intervals while more frequent burning will favor *Q. inopina*.

HABITAT CHARACTERISTICS AND GEOGRAPHIC RANGE OF THE BLUE MOUNTAINS CRYPTOCHIA CADDISFLY (*CRYPTOCHIA NEOSA*). Burr J. Betts, Eastern Oregon State College, La Grande and Robert W. Wisseman, Aquatic Biology Associates, Corvallis, Oregon.

Adult *Cryptochia neosa* males were collected in sweepnet samples and from captivity-hatched pupae from six streams widespread in the Blue Mountains. *C. neosa* is probably the only species of *Cryptochia* in the Blue Mountains and its range may extend further westward and eastward. *Cryptochia* larvae were collected or observed in 128 additional small, low-order, high-gradient streams containing clean woody debris. Larvae cling primarily to submerged wood and bark during the summer, but also move into mats of damp, decaying leaves in the fall. Most habitat characteristics that differed significantly between streams with and without *Cryptochia* can be related to their effect on substrate cleanliness. The type of stream that *Cryptochia* inhabits is receiving better protection in forest management plans. We suggest that the status of this species, related to its potential for listing on the Federal Rare and Endangered Species List, should be downgraded from Category 2 to 3C.

PRIMARY CAVITY EXCAVATOR BIRDS IN GRAND FIR FORESTS OF CENTRAL WASHINGTON'S EAST CASCADES. Kenneth R. Bevis, Central Washington University, Ellensburg.

Populations of Primary Cavity Excavating forest birds are hypothesized to vary with available standing dead trees (snags). Characteristics of selected snags may vary by forest type. Seven plots in a continuum of forest management intensity were measured for PCE bird densities, habitat variables and snag selection. PCE birds selected large diameter snags with advanced decay for feeding and nesting. PCE species composition shifted across the range of plots. Regression models showed total populations as most predictable by density of large snags. Forest management implications are discussed.

Keywords: Excavators, snags.

DISPERSAL AND DEMOGRAPHICS OF COYOTE (*Canis latrans*) PUPS IN SOUTH-CENTRAL WASHINGTON. Jeffrey W. Blatt, Central Washington University, Ellensburg.

This study investigated home range size, sex ratios, dispersal direction and distance, and the causes, and magnitude, of coyote mortality in the first year of life. The pup home ranges increase through the year. Sex ratio's maintained a 1:1 ratio at all time periods. An evident dispersal direction from high to low density suggests dispersal is one population regulating mechanism. Dispersal rate was high. The overall mortality for the first year was high, with more male mortality. The majority of mortality was human caused and outside the natal home range during the dispersal and breeding time periods.

THE COLOCKUM ELK STUDY. Edward Bracken, Washington Department of Wildlife, Ellensburg. John Musser, Washington Department of Wildlife, Wenatchee.

Seasonal habitat preferences of the Colockum elk herd were studied by comparing use (based on locations of radio collared elk) with availability of selected habitat components. Habitat was represented as eight digital data layers (viz., land cover, size and spacing of cover and forage areas, slope, distance from water, roads, aspect, elevation, and land ownership) in a geographic information system on personal computers. Most of the significant habitat relationships identified were related to size and spacing of cover and forage areas, slope, distance from water, and land ownership. A summer elk habitat effectiveness model based on cover-forage area size and spacing, slope, and distance to water was developed and tested.

COMPARISON OF ANIMAL INFECTIVITY, IN VITRO EXCYSTATION, AND FLUOROGENIC DYE AS METHODS TO DETERMINE *GIARDIA LAMBLIA* VIABILITY. Richard Bradley, Central Washington University, Ellensburg.

Giardia lamblia is the most frequently identified waterborne pathogenic protozoan in the United States. Investigators have used several methods to determine the viability of cysts of the parasite. The methods used have included the Mongolian gerbil model, in vitro excystation, and the fluorogenic dyes fluorescein diacetate and propidium iodide. The purpose of this study was to compare these methods to determine their effectiveness in assessing cyst viability. *G. lamblia* cysts were stored in distilled water at 4 degrees celsius, and viability studies were conducted at intervals over 60 days using each of these three methods. Excystation declined steadily after 14 days and may underestimate cyst viability. Fluorogenic dyes required a cyst maturation period to achieve maximum staining. The animal model estimates viability on groups of cysts, but does not provide information on individual cysts.

LONG TERM MAINTENANCE OF WASHINGTON'S NORTH AMERICAN LYNX POPULATION: A LANDSCAPE PLANNING APPROACH. J. David Brittell, Washington Department of Fish and Wildlife, Olympia, Stephen A. Pozzanghera, Washington Department of Fish and Wildlife, Olympia.

The North American Lynx (*Lynx canadensis*) was state listed as a threatened species in Washington by the Wildlife Commission in October 1993. While the distribution of this species in Washington has changed little since the 1920s, lynx population densities have declined and suggest that lynx may now be more vulnerable to habitat loss and alteration than what was historically the case. The opportunity to reverse past negative habitat changes within lynx range are minimal and take considerable time. However, current and future forest management plans can ensure the long term maintenance of lynx, and lynx habitat by providing a mosaic of forest successional stages within the landscape.

COMPARATIVE BIOLOGY OF MONTANE AND LOWLAND POPULATIONS OF *ASCAPHUS* TADPOLES IN NORTHWESTERN WASHINGTON. H. A. Brown, Western Washington University, Bellingham.

Tadpole body size, duration of tadpole life, and size at metamorphosis were analyzed in lowland (elev = 500 ft), montane (1200-2800 ft), and subalpine populations (3500 ft). Most lowland tadpoles require two years and have a large body size at transformation while montane and subalpine tadpoles require three years and have a small body size. Austin Ck (lowland) is unique and shows much diversity; tadpoles have a one or two year larval period with older tadpoles transforming in June at large size and younger tadpoles, in July and August with smaller size; tadpole skin color is black, brown, or tiger stripe (mixture of black, brown, yellow and white), and there is albinism and *situs inversus viscerum*. Subalpine populations are also variable: Yellow Aster Butte shows tadpoles of stunted growth and small body size; Swift Ck has medium size tadpoles that develop for three or four years.

ECOLOGY OF A BEACH POPULATION OF THE WESTERN FENCE LIZARD, *SCELOPORUS OCCIDENTALIS*, IN NORTHERN PUGET SOUND. H. A. Brown, Western Washington University, Bellingham.

A mark and recapture study of fence lizards was conducted from 1986 to 1993 along the eastern shores of Port Susan (about 15 miles north of Everett, WA) to identify annual variations in reproduction, growth, survival, and population stability. Adult activity generally extends from March to September. Mating occurs in late April, and females lay eggs during May or June. Hatchlings (svl 23-25 mm) appear in August-November and grow slowly; juveniles (svl 31-50 mm) grow slowly from March to June and may reach 60-62 mm in September. Some fast growing lizards are sexually mature in the second year (after two hibernations) and others, in the third year. Adult females are larger than adult males, and this is probably due to a greater survival of females. Some lizards live for 6 or 7 years and a few, 8 and 9 years.

EFFECTS OF SITE PREPARATION ON N AND P AVAILABILITY IN A CUTOVER IN NORTHERN INTERIOR BRITISH COLUMBIA. K.R. Brown, Canadian Forest Service, Sault Ste. Marie, Ontario, and D.G. Brand, Canadian Forest Service, Hull, Quebec.

Low soil temperatures and N and P availability may limit the growth of conifer seedlings in plantations in the sub-boreal region. However, treatments which increase soil temperatures by exposing mineral soil may reduce N and P availability. We used ion exchange resins to measure, *in situ*, available $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$ following planting with *Picea glauca* x *engelmannii* (interior spruce) and *Pinus contorta* seedlings near Prince George, B.C.¹. Plots were scarified, fertilized and/or sprayed with herbicide in a factorial experiment. Seedlings were planted in 1987; fertilization and brush control were repeated in 1988 and 1989. Resin bags were placed in the rooting zone from July-August 1989 and June-July and July-August 1990. Total mineral N and P adsorbed by the resins were least in scarified plots and tended to be greater in herbicided plots. Nearly all of the adsorbed N was $\text{NH}_4\text{-N}$. Current-year needle concentrations of N and P in spruce were generally lowest in scarified plots in 1989-1990. Scarification increased spruce biomass through 1988 in association with increased soil temperatures¹; lesser amounts of adsorbed N and P and decreases in foliar N and P concentrations over time indicate longer-term declines in site productivity.

¹Brand, D.G. 1991. Forest Science 37:68-100.

ELEMENTAL DEFICIENCIES IN DOUGLAS-FIR STANDS OF SE BRITISH COLUMBIA. K.R. Brown, Canadian Forest Service, Sault Ste. Marie, Ontario. R.M. Fournier, Ecole de Sciences Forestieres, Edmunston, NB. G.F. Weetman, University of British Columbia, Vancouver.

Deficiencies of several elements, mainly N,P,S and B, may limit the growth of native-stand Douglas-fir, managed for Christmas tree production, in the Rocky Mountain Trench of S.E. British Columbia. Four rates of N (0, 56.7, 113.4 and 170.1 g per tree) as $\text{NH}_4(\text{SO}_4)_2$ (NS) with or without phosphate + boron (PB) were applied at 15 sites in the spring. Probable elemental deficiencies were identified by vector analysis of current-year foliage collected in the fall. The NS regimes increased needle masses and concentrations of N and S. The PB regimes increased needle masses and B concentrations only in combination with the NS regimes. Concentrations, but not needle contents of P, decreased with NS fertilization. Thus, N and S appeared to be deficient; B deficiencies were induced by fertilization with N+S; P was diluted by NS fertilization, but did not limit needle growth.

EFFECT OF LOGGING ON TAILED FROG POPULATIONS IN NORTHEASTERN OREGON. Evelyn L. Bull, U.S. Forest Service, PNW Research Station.

Thirty streams in northeastern Oregon were surveyed for tailed frogs in June and July 1993. A third of the streams fit into each of three logging categories: $\leq 20\%$ of the watershed harvested, 21-50% harvested, and $> 50\%$ harvested. In each stream, a 1,000-m stretch of stream was searched during the day for the larvae, and the same stretch was searched at night for the adults. Several streams contained as many as 700 larvae and 100 adults. Streams with extensive logging and no buffers contained few larvae or adults. Females laid eggs in June or July; hatchlings were found in August; breeding was observed in September and October 1992.

FRESHWATER TURTLES OF THE PACIFIC NORTHWEST: ISSUE OF INTRODUCED SPECIES. R. Bruce Bury, National Biological Survey, Corvallis, OR.

Introduced species of turtles are a potential problem for native turtles and aquatic habitats in western North America. Field observations suggest that there 4-5 species of introduced turtles in WA, 7 in both OR and CA, and 1-2 in British Columbia. Furthermore, some of these species are breeding in the wild. Field studies at Fort Lewis, WA, indicate that red-eared sliders are now the predominate turtle whereas the native species (western pond turtle) is absent. The success of an introduced competitor may be one contributing factor to declines in native turtles, but a cause-effect relationship between abundance of these species needs to be established. Occurrence of sliders and other basking species may seem benign, but introduced turtles have great potential to spread parasites or diseases to native wildlife. Snapping, softshell and mud turtles often avoid detection because they are highly aquatic. These species prey on native fishes and wildlife, and can inflict injury to unwary people.

NATURAL HISTORY AND EVOLUTION OF STREAM AMPHIBIANS IN THE PACIFIC NORTHWEST. R. Bruce Bury, National Biological Survey, Corvallis, OR.

Amphibians are a diverse assemblage and major components of many stream ecosystems. Recent studies suggest that Olympic and giant salamanders are distinct families of amphibians, and the tailed frog is one of the most unique vertebrates in the world. There are now 10 species in these groups and all of them are endemic to the Pacific Northwest. Also, stream amphibians can be the dominate predator of headwaters. Logging may extirpate populations locally or reduce the abundance of species. Negative effects of logging may be lessened by retention of >25% of forest stands in watersheds and, perhaps, by buffer zones. Several of the species merit consideration for protection. An interagency team is needed to monitor population trends and to devise effective management of headwater habitats.

CRYPTOGAMIC SURVEY OF McDONALD-DUNN RESEARCH FOREST. Francisco J. Camacho and Nick Otting, Oregon State University, Corvallis.

The importance of biological diversity is becoming an accepted part of the management of natural resources. McDonald-Dunn Research Forest is interested in knowing its species diversity of cryptogamic organisms. The goals of our study are 1) to catalog the cryptogamic species of McDonald-Dunn Research Forest, 2) to identify sensitive species 3) to establish baseline permanent lichen plots for the long term monitoring of air quality. For the purpose of this study only the lichens, bryophytes, macrofungi, and a few microfungi are considered. The various habitats of the Research Forest are being visited to catalog these organisms. Each specimen collected is identified, ecological data is recorded, and all information is entered into a data base. Also entered into the data base are collections made in the Research Forest from the OSU herbarium and from private collections. At present, over 600 collections, consisting of more than 110 lichen species, 180 fungal species, and 35 bryophyte species, have been entered into a data base. There are over 400 vascular plant species known to occur McDonald-Dunn Research Forest. It is expected that the number of cryptogamic species will exceed that of the vascular plants.

PROTECTION OF PLANTS USED TO INCREASE FOREST DIVERSITY

Dan L. Campbell and Dale L. Nolte, USDA APHIS DWRC Olympia, WA.

Constance A. Harrington, USDA Forest Service, Olympia, WA.

Forest managers in the Pacific Northwest recognize that plant diversity is important for wildlife habitat, riparian restoration, and timber production. Desired species include trees such as western redcedar (Thuja plicata) and bigleaf maple (Acer macrophyllum), and many shrubs, vines, and forb species. Many of these plants are more palatable than Douglas fir (Pseudotsuga menziesii), and if not protected are damaged extensively by wildlife before they become established. We have, and are continuing to evaluate materials and methods to protect these plants using repellents, barriers, and improvement in plant species composition, to alleviate damage from wildlife. One commercial repellent (BGR-P) and an experimental repellent derived from starlings (Sturnus vulgaris) significantly reduce damage to western redcedar. Increased densities of selected forbs have reduced damage to Douglas fir and may benefit other species. Several native plant species are being evaluated to reduce damage to other plants. Barrier materials are selected to accommodate specific growth patterns of the plant species needing protection.

CREATING CAVITIES IN TREES—ONE FACET OF ECOSYSTEM MANAGEMENT. Andrew B. Carey, Pacific Northwest Research Station, USDA Forest Service, Olympia, WA.

Accelerating development of foraging habitat for *Strix occidentalis* (STOC) and enhancing biodiversity entail providing for the primary prey of STOC (*Glaucomys sabrinus*, GLSA) and other cavity-using wildlife. A technique for creating cavities immediately available to GLSA has been developed. Cavities are excavated in live trees using a chainsaw and covered with wooden faceplates. This process should introduce top rot into the tree which should, in time, provide substrate suitable for excavation by picids. Vegetation management can enhance spatial (horizontal and vertical), architectural, and species diversity. Spatial diversity is conducive to avian community diversity and foraging and roosting by STOC. Plant species diversity leads to small mammal diversity. Combining cavities with vegetation management for biodiversity should lead to synergistic effects at the ecosystem level. For example, increasing woody plant species diversity and GLSA numbers should lead to increases in diversity and abundance of ectomycorrhizal fungi (GLSA food and tree symbionts) and ecosystem productivity. Cavity and vegetation enhancement should be combined with coarse woody debris management for best results. These concepts are illustrated in a 15-minute VHS videotape that can be purchased or borrowed.

INTERACTIONS OF NORTHWEST FOREST CANOPIES AND ARBOREAL MAMMALS. *Andrew B. Carey*, Pacific Northwest Research Station, Olympia, WA.

Mammals using forest canopies in the Pacific Northwest are, in order of arboreality (important canopy features): *Arborimus longicaudus* (large *Pseudotsuga menziesii* with large branches; deep, interconnected crowns; epiphytes; fog interception); *Glaucomys sabrinus* (cavities in dead and live trees; epiphytes; *P. menziesii*; diversity of Pinaceae; ericaceous species; multilayering); *Sciurus griseus* (*Quercus garryana*, *P. menziesii* or *Pinus ponderosa*; diversity of mast producing trees and shrubs; interconnected crowns; nearness to water); *Tamiasciurus douglasii* (cavities in live and dead trees; diversity of seed and mast producing trees and shrubs; interconnectedness; epiphytes); *T. hudsonicus* (*Pinus contorta*; diversity of mast and seed producing trees and shrubs; near seeps, springs, or streams); *Martes americana* (cavities, large branches); *Neotoma fuscipes* (hardleaved sclerophylls; woody debris; interconnectedness); *N. cinerea* (cavities and woody debris); *Tamias townsendii* (cavities; diversity of seed and mast producing species). In general, arboreal mammals seem to benefit from large trees (live and dead), cavities, epiphytes (food, nest material), tree and shrub species diversity, interconnectedness of crowns, and canopy layering. Biogeography is important. Niche diversification seems to arise from food specialization; niche overlap is greatest in use of cavities and stick nests.

SOME ZOONoses POSING RISKS TO FIELD BIOLOGISTS IN THE NORTHWEST. *Andrew B. Carey*, Pacific Northwest Research Station, USDA Forest Service, Olympia, WA.

Numerous microorganisms that infect wild animals (zoonoses) also can infect humans. Biologists' concerns about contracting zoonotic diseases have increased because of recent deaths due to hantavirus. But biologists are at risk from many zoonoses transmitted by or in ticks (Lyme disease, Colorado tick fever, Rocky Mountain spotted fever); fleas (bubonic plague); mosquitos (western equine encephalitis); animal urine, feces, and aerosols (hantavirus, histoplasmosis, leptospirosis); blood and other tissues (bubonic plague, tularemia, tapeworm); saliva (rabies); and water (giardiasis). Awareness of diseases enzootic in study areas, prophylactic work habits, common sense, and good personal hygiene can go a long way towards preventing contraction of diseases. Exposure to pathogens during general field work can be reduced by wearing coveralls (taped at wrists and cuffs to exclude ticks) in the field, but not into the office or home; mosquito repellent; and latex surgical gloves (when handling animals, bedding, and traps); refraining from eating, drinking, and touching eyes, nose, mouth, and genitals while handling potentially contaminated objects until hands are thoroughly washed; periodically searching one's body for ectoparasites; and employing other indicated prophylactic measures (vaccinations, respirators).

ECOSYSTEM MANAGEMENT: AN EXPERIMENT IN MANAGED STANDS. *A.B. Carey, T.M. Wilson, T.B. Thomas*, PNW Research Station, Olympia, WA., *J.M. Trappe*, and *W. Colgan III*, OSU, Corvallis, OR.

Recent research has shown that arboreal and forest-floor small mammals are more abundant in old-growth than in young forests. Differences in abundance of fallen trees, snags, and understory development can account for much of the variability in mammal populations across old and young stands. We have shown that spotted owl habitat use reflects mammalian prey abundance and degree of understory development. Our hypothesis is that by manipulating young managed stands by creating cavities in live trees to benefit flying squirrels and other cavity users, and by creating three levels of overstory tree density to promote understory diversity and tree growth we will produce synergistic effects on trophic pathways among plant, fungal, invertebrate, and vertebrate populations that restore many characteristics of late-successional forests. This experiment is a randomized block design with 4 replicates of 4 treatments: cavities and nest boxes added, variable-density thinning (and planting), cavities and thinning, and no intervention. Cavities and nest boxes treatments were applied in 1992, variable-density thinning treatments were applied in 1993. A study precis is available upon request.

CANOPY FUNGI: FUNCTION AND DIVERSITY. *George C. Carroll*, University of Oregon, Eugene.

Forest canopies provide substrates for a diverse array of ascomycetous fungi, yeasts and bacteria. The fungi fall into several distinct functional groups. Epiphytic fungi live superficially on leaf and bark surfaces and serve to concentrate dilute organic materials, thus providing food for canopy microarthropods. A wide range of saprotrophic decomposers probably break down perched litter; some of these produce tetra-radiate spores typical of aquatic hyphomycetes. Fungal endophytes live asymptotically within the stem and leaf tissues of many trees. While individual infections in healthy tissues are invariably limited, these fungi may proliferate when tissues are stressed or wounded. A number of these species have been found to produce compounds toxic to insects. Field studies with Douglas fir and Garry oak have shown that endophytes can invade leaf galls and kill the larvae of galling insects. Thus, some fungal endophytes appear exist in mutualistic associations with their hosts.

EFFECTS OF LIVESTOCK REMOVAL ON VEGETATION OF THE SANDY RIVER DELTA, TROUTDALE, OR. Linda Cartwright, Mt. Hood National Forest, Fred C. Hall, USDA Forest Service, Pacific Northwest Region.

A study to evaluate the effects of livestock removal on vegetation of the Sandy River Delta, near Troutdale, Oregon, was started in March, 1992. Thirty-three photo points were established where foliar cover by species was estimated. Each photo point was sampled the first of every month for 24 months. Removal of livestock resulted in major changes: number of species decreased to 60% of those present under grazing; legumes were eliminated; reed canarygrass increased dramatically; grass thatch seemed to be the major factor causing change in species dominance; grass thatch greatly enhanced rodent habitat and seemed to reduce accipitor activity. We found a problem in how to document foliar cover as it changed from green to dry and how to interpret its environmental influence. Color photography, utilizing three views, helped resolve the problem: 1) A general view 10 meters from a meter board; 2) a picture left and 3) a picture right of the board from a distance of 2 meters.

CURRENT LAND COVER OF THE COLUMBIA BASIN. Kelly Cassidy, WCFWRU, WH-10, U. of Washington, Seattle WA.

The land cover of the Columbia Basin is being mapped as part of the Washington State Gap Analysis Project. Landsat Thematic Mapper (TM) imagery from 1991, with a resolution of 25 meters, is the primary source of land cover data. Each TM scene was spectrally clustered to combine areas of similar reflectance. The scenes were displayed in a GIS system and areas of similar land cover were manually outlined at a minimum mapping unit of 100 hectares. The resulting polygons are being labeled with primary and secondary cover types based on spectral reflectance and ancillary information. A preliminary map of the land cover of the Columbia Basin will be presented, with emphasis on the current status of native vegetation types.

A PRELIMINARY CLASSIFICATION OF FOREST VEGETATION IN THE PUGET TROUGH, WASHINGTON. Christopher B. Chappell and Rex C. Crawford, Washington Natural Heritage Program, Department of Natural Resources.

Our objective was to describe and classify natural forest vegetation in the Puget Trough physiographic province. The classification will be used as a basis for conservation of natural forests in the Puget Trough. We used a hierarchical method that recognizes forest series, plant associations, and distinctive seral communities. Vascular plant species cover data from 292 plots in relatively undisturbed forests were analyzed with TWINSPLAN (a hierarchical classification technique) and DECORANA (an ordination program), and then classified. A dry climatic area (42-75 cm mean annual precipitation) in the northern end of the Puget Trough supports 3 forest series with differing potential vegetation: Tsuga heterophylla (moist sites), Abies grandis (mesic sites), and Pseudotsuga menziesii (dry sites). The remainder of the Puget Trough receives 75-200 cm annual precipitation and apparently lacks the intermediate Abies grandis series. Arbutus menziesii is an indicator species that dominates a portion of the P. menziesii series. A number of plant associations emphasizing dominant understory species are described, based on data from mature and old-growth plots. P. menziesii dominates or co-dominates the vast majority of natural forests in the province. Alnus rubra and Pinus contorta form short-lived seral communities.

TROPICAL FOREST CANOPY ACCESS AND ORGANISMS, AN INTRODUCTION. Joel Clement, The Canopy Institute, Olympia, Washington.

An understanding of the ecology of temperate forest canopies can be greatly enhanced by comparative data obtained from tropical canopy ecosystems. A discussion of canopy access techniques and experiences on the Osa Peninsula in Costa Rica provides potential tropical investigators with information on what to expect and how to find what you're looking for. Topics will include general canopy and crown characteristics, typical plant and animal associations, low-impact access and special precautions, coordinating with local communities, and a brief description of a remote field station in Costa Rica. Accompanied by a slide presentation.

PRELIMINARY ECOLOGICAL OBSERVATIONS OF *UROPHORA AFFINS*. Valery Companytsev and Richy J. Harrod, U.S.D.A. Forest Service, Leavenworth, WA.

The fruit fly *Urophora affinis* is used for biological control of diffuse knapweed (*Centaurea diffusa*). Larvae form multiple galls (one larva per gall) in the receptacle tissue of the immature flower heads. The ecological characteristics of the interactions between fly and plant populations are being examined. During summer of 1993, a study was designed using several plots at different elevations to determine flies distribution and larvae density on white- and purple-flowered plants. Using nonparametric statistical methods we found significant differences in the extent of parasitism between elevations. However, there was no significant difference in larvae abundance between white and purple color morphs (mean of 1.44 and 1.39 per head, respectively). In addition, we analyzed eight morphological characteristics of male and female flies collected from individual white- and purple-flowered plants. Initial results suggest no differentiation between morphological guilds (wing and head shape) by color morph or individual plants within a morph. These results suggest that the inferred genetic structure of *C. diffusa* does not influence the inferred genetic structure of *U. affinis*, and that variation within fly populations is likely dependent on ecological factors (i.e. environmental variables at different elevations).

IDENTIFYING OREGON AMPHIBIANS IN THE FIELD: NEW INFORMATION FROM THE FIELD WORK. Charlotte C. Corkran and Chris Thoms, Northwest Ecological Research Institute, Portland.

Preparation of a manual for identifying live amphibians in the field in Oregon yielded some new information on several species and led to some new methods for distinguishing between related species. Three years of extensive field work and photography, with limited captive raising and examination of museum specimens, enabled comparison of many species over a range of developmental stages. Distinguishing between larger larvae of Cope's Giant Salamander (*Dicamptodon copei*) and Pacific Giant Salamander (*D. tenebrosus*) is possible using head shape, external gill proportions, and leg length rather than counts of vomerine teeth and gill rakers. The vent orientation of anuran larvae in early development stages is manifested in the symmetry or asymmetry of the body. Foothill Yellow-legged Frog (*Rana boylei*) larvae were found to have adaptations to moving water similar to those of Tailed Frog (*Ascaphus truei*) larvae. Several wetland plant associations may be indicators of the presence of certain amphibian species. The hatchling and larger larvae of both salamanders and anurans can be distinguished by external structures, proportions, and other visual clues, rather than by methods which require dissection or which frequently damage or kill individuals.

COMMON FACTORS AND CONTRADICTIONS IN AMPHIBIAN DECLINES. P. Stephen Corn, National Biological Survey, 4512 McMurry Avenue, Fort Collins, CO 80525-3400.

Boreal toads (*Bufo boreas*) have declined 80-90% in the southern Rocky Mountains. The relict Wyoming toad (*B. hemiophrys baxteri*) is nearly extinct in southern Wyoming. The declines of these species share some common features that might suggest a common cause. Both species apparently declined during the same period—since about 1975. Red-leg disease has been observed in both species. Surviving populations of both species show some similarities in demography, including low numbers of egg masses relative to adult population size. The natural histories of these toads differ in several important features, however. *Bufo boreas* and *B. hemiophrys baxteri* are allopatric, occur over different ranges of elevation, and use different types of habitats. Other species of anurans in the same habitats have not declined. Acidification, the only broad-scale factor examined to date, is unlikely to have caused the decline of either species.

INFLUENCE OF WATER USE PRACTICES ON FISHERIES RESOURCES IN THE YAKIMA RIVER BASIN. Dennis Dauble, Pacific Northwest Laboratory, Richland, Washington.

Human activities during the last century have caused dramatic changes in salmonid populations in the Yakima River basin. Declines in fish populations can be linked to increased use of surface water supplies for agricultural, domestic, and industrial purposes. Six storage dams currently help provide irrigation water to nearly a half-million acres of cropland in the Yakima River basin. Diversion of water into the irrigation system reduces flow, and the demand of water used for farming and ranching sometimes exceeds the supply. Irrigation return flows also contribute to increased temperatures, high levels of dissolved solids, and residual contaminants in the lower river. Several management agencies recently initiated efforts to assess the significance of stream flow and water quality conditions to aquatic life. Collectively, these studies indicate that instream flows are a major constraint to anadromous fish production. Water temperature may also limit production of salmonids in the late summer. An evaluation of water quality criteria, which considers salmonid life history requirements, has been developed to help guide strategies for mitigating conditions that adversely affect fisheries resources.

ASCOSPORES OF LOBARIA. William C. Denison, Oregon State University, Corvallis.

Two species of Lobaria are common in western Oregon, L. oregana and L. pulmonaria. Both reproduce asexually; L. oregana by lobules, L. pulmonaria by soredia. Both may also produce ascospores. Only a few large, mature-looking thalli have apothecia, but they are long-lived, continuing to expel ascospores over periods of weeks or months. Apothecial color changes over time, from pale tan to black. An excised apothecium, on moist filter paper, at cool temperatures, will shoot ascospores onto a cover glass or agar placed above it for several days. Apothecia with ascospores are found throughout the year. Ascospores of both L. oregana and L. pulmonaria are fusiform, with a median septum, or with one or more others. Ascospores do not germinate on common agar media, with or without added nutrients. Evidence suggests that germination is blocked by an endogenous inhibitor.

LICHEN TRANSPLANT EXPERIMENTS USING Alectoria sarmentosa, Evernia prunastri and Lobaria pulmonaria IN WESTERN OREGON. Chiska C. Derr, Oregon State University, Corvallis.

Easily assembled lichen transplants could facilitate studies of basic lichen ecology and be useful for air quality studies. Removable pendants of the fruticose lichens Alectoria sarmentosa and Evernia prunastri and the foliose Lobaria pulmonaria were constructed using 5 cm lengths of monofilament with a 2 cm loop at one end. The monofilament was glued to a 2.5 g lichen thallus with silicon sealant. The transplants were attached to tree branches using "Goody ponytailers," elastic loops with labeled 1 cm plastic beads on each end and a silicon-covered metal crimp in the middle. Transplants were weighed every 3 months for 1 year. Lichen were air dried in the lab before each weighing. Reference standards for each species were used to correct for changes in lichen water content due to changes in lab humidity. Alectoria transplants were returned to their original Noble fir (Abies procera) stand near the summit of Mary's Peak. Alectoria proved unsuitable for transplanting; nearly all transplants lost biomass due to fragmentation of the thallus (-9% biomass change, $s=9$). Evernia and Lobaria were returned to their original habitat, open-grown Oregon white oak (Quercus garryana) in Chip Ross Park, Willamette Valley foothills. Both species were also placed along a 20 mile transect in oaks on the Willamette Valley floor. Average biomass gain was 31% for Evernia ($s=14$), and 13% ($s=10$) for Lobaria. Air quality may be responsible for the absence of Lobaria along the Willamette Valley transect.

AN EVALUATION OF METHODOLOGIES USED FOR SAMPLING WARMWATER FISH POPULATIONS. Marc Divers, Central Washington University, Ellensburg.

The major assumption for any fish population index value to be considered accurate is that the data used for calculations is representative of the entire population. Three sampling methodologies were used to sample warmwater fish populations in order to examine the variability of data collected. The specific objectives are to determine the accuracy of using boat electrofishing for determining Proportional Stock Densities (PSD's), boat electrofishing and multiple mark-and-recapture for making population estimates, and boat electrofishing, experimental gill netting, and fyke netting to determine species composition. Three small lakes in Eastern Washington were repeatedly sampled from May 1993 to October 1993. Proportional Stock Densities were calculated for largemouth bass, yellow perch, and pumpkinseed sunfish. Population estimates were made for each study site. Species composition was determined for each location. These population indices are to be analyzed to determine the amount of variability between individual sampling efforts. Preliminary results show differences in PSD's calculated for largemouth bass, yellow perch, and pumpkinseed sunfish. Differences are also evident between species composition results as determined using these sampling methods.

THE TIGER SALAMANDER (Ambystoma tigrinum) IN THE COLUMBIA BASIN OF EASTERN WASHINGTON. Frederick C. Dobler, Washington Department of Wildlife, Olympia WA.

In the summers of 1992 and 1993, 48 ponds were seined with a six meter hand held seine, to determine presence of tiger salamanders. The main objective was to gain information about distribution and insight into management needs and potential problems. Fifty percent of the waters yielded specimens, mostly non-neotenic larvae, although one neotenic larvae was captured and several transformed adults. Two hundred and sixty-nine captured specimens were measured. Size ranged between 4 and 21 cm. The largest specimen was the neotenic larva. The distribution seems to be mostly limited to small temporary ponds and larger waters lacking populations of large fish. The Columbia Basin Irrigation System has probably created suitable habitat and a means to distribute tiger salamanders in the Columbia Basin.

VEGETATION OF THE BEAVER CREEK
NATURAL RESOURCES CONSERVATION
AREA. Diane S. Doss and Ronald J. Taylor,
Western Washington University, Bellingham.

A baseline botanical inventory of the 62-hectare Beaver Creek NRCA, 8 km east of Bellingham, was performed for the Department of Natural Resources. Terrestrial vegetation was sampled on 46 15x25 m plots and on 2 transects across the site. Two-way indicator species analysis (TWINSPAN) and detrended correspondence analysis (DECORANA) were used to classify and ordinate the plot data. At least 11 community types were recognized, ranging from old growth Douglas fir to alder slopes, an alder/spruce bottom, and alder and cedar swamps. Vascular understory cover ranged from 6% to 232%. DECORANA related some of the community types to soil moisture and topographic position; fire and selective logging in the late 1800s may also contribute to the diversity of vegetation. 133 vascular plant and 39 bryophyte species were found. No federal or state listed species were seen. Of the 11 exotic species found, only wall lettuce (*Lactuca muralis*) and holly (*Ilex aquifolium*) have wide distribution.

RETENTION OF THE PROCESSING PROTEASE
KEX2P IN YEAST IS ALTERED WHEN ITS NATIVE
LUMENAL SPACER, TMD, AND CYTOSOLIC
TAIL ARE REPLACED WITH DOMAINS FROM A
HUMAN HOMOLOGUE. Amy Drake,
Alison Farrell, Cheryl Phillips, Julja Gleason,
and Michael Gleason, Central Washington
University, Ellensburg.

Preliminary results indicate that a chimeric membrane-bound yeast-human prohormone processing protease (*Kex2p-furtail*) is localized differently in the secretory pathway of the yeast, *Saccharomyces cerevisiae* than the native prohormone processing protease (*Kex2p*). Normal and chimeric gene products were expressed in a *MAT α kex2 Δ pep4 prb1 prc1* yeast strain type CB017, in identical CEN $\blacktriangleright$ ARS plasmids under GAL1 promoter control. Localization of normal and chimeric gene products in yeast cells were assessed by immunofluorescence microscopy, cellular assay of prepro- α factor production, and colorimetric assay of fractionated cells for specific in vitro protease activity against Z-Tyr-Lys-Arg-pNA.

AUTOGAMY IN *OROBANCHE PINORUM*. Mark Ellis, Western Washington University, Bellingham; Ronald Taylor, Western Washington University, Bellingham; and Richy Harrod, USFS, Leavenworth.

We began a study of the pollination biology and life history of *Orobancha pinorum* during the summer of 1993. *O. pinorum* is a parasitic species in the Orobanchaceae family of herbaceous root parasites. Although said to be "widespread" in some floras, it is listed as 'sensitive' in Washington State. The literature suggests its hosts are conifers, but *O. pinorum* in the Leavenworth area appears to parasitize *Holodiscus discolor* exclusively. We found *O. pinorum* to be primarily self-pollinating (if not exclusively). Flowers bagged to exclude pollinators produced as many seeds as unbagged flowers. Important pollinators have not been observed. By anthesis, one or more anthers often contact the stigma before releasing pollen, ensuring selfing. Two herbivores have been observed--the larval stages of a fly that attacks the haustorial tubercle, and of a moth that attacks the stems, flowers, and fruits. Monitoring plots have been set up to study ecological associations.

SURVIVAL AND GROWTH OF CONIFERS
RELEASED FROM ALDER DOMINATED
COASTAL RIPARIAN ZONES. W.H. Emmingham, Kathleen Maas, Adaptive COPE,
Oregon State University, Newport.

Five alder dominated riparian zones in the Oregon Coast Range were selected to study release of 261 conifers overtopped by fast growing alder. Douglas-fir, western hemlock and western redcedar seedlings and saplings were released by cutting or girdling alder around the release tree within a radius equal to 1/4 of the total height of the alder stand. Mean survival ranged from 73 to 95 percent on the 5 sites but did not vary significantly by site. Western redcedar had better survival (95%) than western hemlock (75%), but was not significantly greater than Douglas-fir (78%). Mean survival for Douglas-fir and hemlock was greater where overstory trees were girdled or cut. Overstory removal tended to increase both diameter and height growth but only diameter growth showed significant differences. Releasing of riparian zone conifers appears to be a viable option for enhancing conifer survival and growth, thereby contributing to stream rehabilitation.

BAT ACTIVITY IN MANAGED FORESTS OF THE SOUTHWESTERN CASCADE RANGE. Janet L. Erickson, College of Forest Resources, University of Washington, Seattle.

Bats of the Pacific Northwest roost statistically more often in old than young forest. Current forest practices in this region, however, are rapidly converting old growth forests into intensively managed Douglas-fir stands. To assess habitat use of bats across a gradient of managed forest conditions (clearcut 3-7 yrs., sapling-pole 10-12 yrs., and mature 50-65 yrs. stands), an echolocation call survey was conducted on 15 sites (5 per condition) during August 1992. Over 1,014 echolocation calls were recorded and analyzed using divide-by-10 ultrasonic detectors and signal processing software. Comparisons of activity patterns between species indicate differential habitat use. Detections of *Myotis* species (66.7%) were twice as great in mature stands than in clearcut and sapling-pole stands combined. Big Brown bats (97.8%) and silver-haired bats (71.6%) were detected most frequently in clearcut stands with no detections recorded in mature stands. Patterns of activity and feeding rates suggest mature stands are being used as roosting areas while clearcut and sapling-pole stands are used as foraging areas.

USE OF SIGNAL PROCESSING SOFTWARE FOR ANALYSIS OF BAT VOCALIZATIONS. Janet L. Erickson, and Stephen D. West, Wildlife Science Group, College of Forest Resources, University of Washington, Seattle.

Bat researchers have had few options for analyzing high frequency vocalizations produced by echolocating bats. In the past, such data were analyzed using an oscilloscope display of calls presented by a zero crossing period meter. Use of an oscilloscope, however, was difficult given the brevity of the calls. Recently, a system specifically designed for analyzing bat vocalizations, Anabat II, was developed. Anabat II converts analog recordings obtained from count down bat detectors to a digital format which can be displayed on a computer screen as a function of frequency and time (sonogram). Each detection can then be analyzed, edited, and saved as a file thereby generating a library of calls. This system is not appropriate for detailed call analysis because of the loss of harmonic and amplitude information. It has, however, proven to be a valuable tool for identification of species or groups of species based on their echolocation calls.

DEVELOPING A SCIENCE BASIS FOR ECOSYSTEM MANAGEMENT. Richard L. Everett, and Paul E. Hessburg, U.S. Forest Service, PNW Research Station, Center for Sustainable Forest and Rangeland Ecosystems, Wenatchee, WA.

Ecosystem management requires the development of an information base on historical and current ecosystem conditions at multiple hierarchical landscape scales. In the recent Eastside Forest Ecosystem Health Assessment we found forest ecosystems continually shifted in composition, structure, and function with or without human intervention. Current management practices that have created ecosystem conditions outside of their historical range of variability include fire suppression, timber harvest, and grazing. Hierarchical landscape management conducted in an adaptive management process may provide positive cumulative effects that restore desired ecosystem attributes. Integration of public expectations with the biological capability of ecosystems is needed to protect future biological and socioeconomic options.

LICHENS IN FELLFIELDS IN ALPINE MEADOW COMMUNITIES ON THE BEARTOOTH PLATEAU, MONTANA AND WYOMING. Sharon Eversman, Montana State University, Bozeman.

I recorded lichen cover on four fellfields, or cushion plant communities, in alpine meadows on the Beartooth Plateau on the border of Montana and Wyoming. Elevations were from 3000 to 3400 m, above timberline. Of the total vegetation cover, 16.9 to 29.0% was lichen cover on rock; 2.9 to 10.7% of the total vegetation cover was lichen cover on soil and litter. Thirty-six species were recorded from the sampled plots in fellfield communities; 75 lichen species have been identified from communities at krummholz timberline and above. Thirteen saxicolous species were on all four fellfield sites. Coelocaulon muricatum was the only terricolous species on all sites sampled. I have found Evernia divaricata only in fellfields. The lichen cover present indicates that the fellfields probably have less than 50 cm of snow per year and more than 12 snow-free weeks per year.

Differences in Ectomycorrhizal Fungi Densities and Soil Properties in Forest Soils of Northwest Wyoming. E.L. Falen-Rowan, P.A. McDaniel, A.L. Falen, University of Idaho, Moscow, D.S. Page-Dumroese, USFS, Moscow, K.E. Houston, USFS, Cody

Ectomycorrhizal fungi are indicators of forest soil productivity. This study's objective is to correlate soil properties with ectomycorrhizal fungi densities on two paired sites in northwest Wyoming. Four sites were chosen in the *Abies lasiocarpa*/*Vaccinium scoparium* habitat type with similar slopes and aspects. Two sites have volcanic parent material, and two have granitic parent material. The sites are divided into two elevational groups (2530 to 2591 m, 2682 to 2804 m). Average ectomycorrhizal fungi densities vary from 4.6 to 0.3 ectomycorrhizal short tips per gram of root, with highest densities at lower elevations. Phosphorus retention ranges from 73% to 9%, with highest retention occurring at higher elevations. Soil pH's range from 5.4 to 3.4, with more acidic pH's occurring at higher elevations. Sodium fluoride pH, an indicator of poorly crystalline hydrous oxides of iron and aluminum, is highest at higher elevation sites. Differences in ectomycorrhizal densities and soil properties appear to be more related to elevation rather than parent material.

WATERSHED ANALYSIS FOR WILDLIFE SPECIES. William L. Gaines and Richy J. Harrod, US Forest Service, Leavenworth, Washington.

Watershed analysis is becoming a central focus of ecosystem management. However, assessment methods for wildlife and their habitat are still in the developmental stage. We present an assessment of wildlife and their habitats in the Mission Creek watershed on the Wenatchee National Forest. Our assessment proceeded as follows: 1) determine the wildlife species and guilds, 2) use available literature and inventory data to define habitat relationships, 3) assess the current condition of the wildlife populations and their habitats, 4) assess the natural range of variability of the wildlife populations and their habitats, 5) compare the current condition to the natural range of variability, 6) identify restoration projects, 7) implement and monitor. By using this process we estimated the effects of past management activities such as timber harvest, fire exclusion, grazing, and road construction on wildlife habitats. We identified restoration projects such as prescribed fire, snag creation, thinning, and wetland rehabilitation to restore wildlife habitats to within their range of natural variability.

"THROUGH THE EMERGENT ZONE, Documenting Forest Giants of the Pacific N.W."

15 minute video by R. Steve Foster, Filmmaker, Portland, OR

"THROUGH THE EMERGENT ZONE" accompanies researchers and climbers as they ascend to inventory and document some of the largest trees in the world. This documentary takes the audience on a journey above the forest floor into the rarely visited canopy of these ancient trees. The viewer moves through the emergent zone of these forest giants to their 300 foot plus summits as the climbers collect data on these rapidly dwindling specimens.

RARE PLANT PROTECTION IN WASHINGTON STATE: IS THERE A ROLE FOR REINTRODUCTION, TRANSLOCATION AND MITIGATION? John G. Gamon, Washington Natural Heritage Program, Department of Natural Resources, Olympia.

Although many protection methods are available for Washington's rare vascular flora, ongoing threats, primarily the loss and degradation of remaining habitat, continue to challenge our ability to maintain viable populations into the future. The possibility of active intervention is explored in light of recent literature that addresses reintroduction, translocation and mitigation. Positive and negative aspects, as well as limitations, are discussed. The need to develop long range plans that include a clear statement of objectives and which address strategic, administrative and biological questions is emphasized. A few examples of projects in Washington that are either underway or under consideration are briefly mentioned. Future needs are discussed.

STAND AND LANDSCAPE-LEVEL BIRD-HABITAT
ASSOCIATION MODELS IN FOREST PLANNING.
Steven L. Garman, Oregon State University, Corvallis.

Understanding the potential effects of management practices on indigenous vertebrate species is an essential component of the forest management planning process. For this purpose, statistical stand-level habitat models associating occurrence of bird species with vegetative structure have been developed from empirical studies in the Oregon Cascades and Coast Range. Output from stand-level dynamics models which simulate effects of silvicultural options are used with these habitat models to determine trade-offs between timber production and bird-species diversity. Applications for the western OR Cascades have shown retention of green-trees even at low levels to substantially improve bird-habitat diversity with only a nominal reduction in timber volume. Initial use of these bird-habitat models based on a large set of structural variables, however, resulted in spurious results owing to a high degree of autocorrelation with the original field data. Use of a parsimonious set of meaningful variables was found to obviate the potential for erroneous results. Coarse-scale spatial models based on life-history attributes (e.g., minimum patch size) from literature reports were developed to evaluate bird-habitat suitability at landscape scales over a 400yr planning period. Initial results in the Augusta Creek Watershed area indicated the landscape design that best supported adequate amounts of suitable habitat for all species over the planning period. The degree to which results are sensitive to uncertainty in model parameters is currently being evaluated.

ESTABLISHMENT OF AN AIR QUALITY
BIOMONITORING PROGRAM USING LICHENS ON THE
TONGASS NATIONAL FOREST, SOUTHEAST ALASKA.
Linda H. Geiser, USDA-Forest Service, Siuslaw
National Forest, Corvallis, Oregon.

Elemental analysis of 366 samples of four common lichens (*Alectoria sarmentosa*, *Cladonia rangiferina*, *Hypogymnia enteromorpha*, and *Lobaria oregana*), and a forest-wide inventory of the macrolichens and their habitat characteristics at 176 standardized sites were completed. Baseline values for S, N, P, K, Ca, Mg, Al, Fe, Na, Mn, Zn, Cu, B, Pb, Ni, Cr, and Cd were established. The four species had distinctly different elemental baseline ranges. All values were within expected background ranges for non-industrial locations and comparable to values available from other National Parks and Forests, except Ca, Mg, K and Mn, which may be enhanced by marine influences. Species sensitive to sulfur dioxide were widespread and healthy. 425 lichens, mainly macrolichens, were documented. 64 were considered rare. Twenty range extensions are reported including the first records of *Rhizocarpon praebadium* and *Allantoparmelia sibirica* in North America. Macrolichen communities of typical Forest habitats were described. Combining elemental analysis with presence/absence of expected species should provide a sensitive tool for detecting changes in air quality in the future or around present point sources.

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LICHEN COMMUNITIES IN ALPINE REGIONS
OF WASHINGTON STATE Katherine A. Glew
Department of Botany KB-15, University of
Washington, Seattle.

Alpine lichen communities in the Olympic National Park, the surrounding peninsula and the north Cascades Mountains are currently being studied. A comparison of terrestrial and saxicolous lichens from several locations and sites is included. Sampling for community structure was done in the Olympic National Park and the Buckhorn Wilderness area, using a 100m transect across an elevation gradient. Elevation, slope, aspect, substrate and coloration of thallus were noted. Ten random points were selected along the transect to determine the location of lichen communities. At each of the ten points, ten 10cm² subquadrats were randomly selected from a 0.5m² quadrat. Percent cover of lichens was recorded. Analysis using DCA and CANOCO was done to determine relationships between species, samples and environmental data. Substrate and vegetation cover demonstrated strong correlations with lichen species distribution. Aspect, slope and elevation did not appear to be strong environmental influences affecting distribution of lichens studied in the Olympic Peninsula. Paler lichens displayed a high association with vegetation patches. Ground patterning and stability of substrate were factors that affect the distribution of lichens.

THE HANTAVIRUS ASSOCIATED PULMONARY SYNDROME. Marcia Goldoft, Washington State Department of Health.

A recent outbreak in southwestern United States led to the recognition of hantavirus pulmonary syndrome (HPS). This severe pulmonary illness occurs in previously healthy individuals and has been associated with a new species of hantavirus (Meurto Canyon) carried by the deer mouse (*Peromyscus maniculatus*). Previously identified hantaviruses are also rodent borne and are responsible for kidney disease in humans. DNA fingerprinting suggests the new virus is genetically diverse. The first HPS case was identified retrospectively from 1990; 53 known cases have been reported from 14 states with 74% occurring April-July 1993. The HPS cases range in age 12-69 years. The syndrome involves a short flu-like illness followed by rapid respiratory distress syndrome requiring ventilation. There have been 32 deaths. Although neither human cases or infected mice have been identified in Washington State, fatal cases and infected mice have been found in both Oregon and Idaho.

STRUCTURE AND DYNAMICS OF MULTIPLE AGE CLASS CONIFER STANDS IN THE OREGON CASCADES. Matthew N. Goslin, Thomas A. Spies, Oregon State University, Corvallis.

Two stands, characterized by the presence of distinct age classes, are being studied with the aim of describing succession after partial disturbances as contrasted with that after catastrophic disturbances. We also aim to describe potential outcomes of green tree retention cuts advocated in current forest management. Remnant trees (300-600 yrs), survivors of multiple fires, are dispersed among a regeneration class (<95 yr) originating after the most recent partial burn. Reference stands (2ha) were established, all trees being mapped and input into a geographic information system (GIS). In the regeneration class, chinquapin (*Castanopsis chrysophylla*) and western hemlock (*Tsuga heterophylla*) appear to be aggregated and Douglas-fir (*Pseudotsuga menziesii*) disaggregated relative to the remnant tree distribution. Regressions of individual tree growth relative to a distance-dependent remnant tree competition index demonstrate a significant, but weak (low r^2) negative association for Douglas-fir and positive association for western hemlock. At present, the data suggest that remnant trees affect regeneration growth on an area basis more strongly than on an individual tree basis.

HANTAVIRUS RISK FACTORS, RODENT RESERVOIRS AND PREVENTION MEASURES. John H. Grendon, Washington State Department of Health.

Hantavirus cases in 16 states are likely associated with domestic, occupational or leisure activities which resulted in contact with infected rodents. Studies are being conducted to identify specific risk factors that may increase the risk of hantavirus infection in humans. The primary reservoir for the newly recognized hantavirus in the Western U.S., the deer mouse (*Peromyscus maniculatus*), has a wide geographic range including all Washington counties. Seropositive deer mice have been found in states with confirmed human cases, including Oregon and Idaho. Limited rodent testing in Washington has not identified seropositive rodents. Reducing the risk of rodent exposure in the home and other settings using rodent control procedures is the best prevention. Persons frequently exposed to rodents need to follow enhanced precautions.

FOREST STEWARDSHIP EDUCATIONAL PROGRAM Donald Hanley and David Baumgartner Washington State University

There has been a significant change in forestland management practices in the state of Washington. Increasingly large numbers of foresters and non-industrial private forest (NIPF) landowners are now managing for stewardship values. This change is in part a result of the Forest Stewardship Educational Program offered by WSU's Cooperative Extension. Working with agents from the DNR and other natural resource professionals, an integrated forest stewardship curriculum was developed. This curriculum includes 68 programs, a comprehensive Stewardship calendar mailed to over 16,000 NIPF landowners, and *Forest Stewardship Notes*, an informative newsletter mailed 3 times a year. The Forest Stewardship Program is an example of effective issue-based programming. It facilitates NIPF landowners' efforts to change from a commodity- to ecosystem-based management approach. Over 1,500 NIPF landowners attended at least one of the workshops. Future events will permit landowners to write their own stewardship plans through a "coached-planning" approach.

ESTABLISHMENT VS. PERSISTENCE
STRATEGIES IN DIMORPHIC LEAVES OF
ACACIA KOA. David H. Hansen, Pacific Lutheran
University, Tacoma.

Predictions of comparative characteristics in leaves that function for establishment versus those leaves that function for persistence in environments that are periodically stressful were tested for leaf types of koa (*Acacia koa*) in Hawaii Volcanoes National Park. Among characteristics compared in the field were gas exchange parameters, carbon 13 discrimination, carbon/nitrogen concentrations and leaf water-potential. All comparisons fit the general predictions. It is concluded that a large amount of the differences between leaf types can be explained by differences in leaf morphology and angle of presentation relative to the sun. This tends to support an hypothesis that within broad physiological categories (i.e. C₃ vs. C₄), adaptation to variations in environment tend to be handled by variations in morphology.

THE SEASONAL DISTRIBUTION OF THE
TRICHOPTERA OF YAKIMA RIVER.
M. Hardwick, Central Washington University,
Ellensburg. S.D. Smith, Central Washington
University, Ellensburg.

The caddisfly adults of the Ellensburg reach of the Yakima River were surveyed and the periodicity of their occurrence was recorded. Eighteen species were collected during 1993. The collection dates spanned from May to October with peak emergence in June and July. Those species that occurred in the greatest as adults were *Glossosoma velona*, *Hydropsyche occidentalis*, and *Psychomyia flavidula*.

A PRELIMINARY REPORT ON THE
PHYTOGEOGRAPHY AND ECOLOGY OF THE
MOSSES WITHIN THE SAN JUAN
ISLANDS, WASHINGTON. Judith
Strachen Harpel. Department of
Botany, University of British
Columbia, Vancouver, B. C. V6T
1Z4.

Floristic work on bryophytes in the state of Washington has been confined mostly to the mainland with little information available for the San Juan Islands. Over a period of four years bryophytes and various lichens were collected within the islands along with detailed habitat data. This work resulted in a total of 221 species of mosses. These mosses represent two different interesting patterns, one represented by southern or northern elements at or near their distributional limits, the other disjuncts with affinities to North America or Asia.

A COMPARISON OF THE FOOD HABITS AND
MICROHABITAT USE OF WILD AND
HATCHERY-REARED RAINBOW TROUT
(*ONCORHYNCHUS MYKISS*) IN THE
TEANAWAY RIVER. David D. Harper, Paul W.
James, Central Washington University,
Ellensburg.

The proposed supplementation of declining wild anadromous salmonid stocks with hatchery-reared fish has raised many questions about what effects these fish will have on the resident fishes. Two critical factors in determining resource partitioning and species composition are food and microhabitat use. We examined fish stomach contents, and snorkeled to determine the microhabitat use of wild rainbow trout and hatchery-reared steelhead smolts. The North Fork Teanaway River which received an experimental release of 30,000 hatchery-reared steelhead smolts and contains a population of wild rainbow trout served as the study area. The Middle Fork Teanaway which also contains wild rainbow trout but did not receive supplementation served as the control.

CHARACTERISTICS AND DISPERSAL OF
CYPRIPEDIUM FASCICULATUM SEEDS. Richy J. Harrod USDA Forest Service, Leavenworth, Wa.

The seed morphometry and dispersal of the rare orchid *Cypripedium fasciculatum* was examined. Seeds are clear with brown netting, have a mean length of 1.41 mm and width of 0.18 mm and have a volume of $12 \text{ mm}^3 \times 10^{-3}$. Embryos are yellow brown, have a mean length of 0.17 mm and width of 0.12 mm and a volume of $1.3 \text{ mm}^3 \times 10^{-3}$. Seed volume to embryo volume ratio is low compared to other *Cypripedium* spp. Seeds are also buoyant ($\bar{x} = 10.9 \text{ s}$ to fall 1.5 m), nearly twice as much reported for *C. calceolus*. A seed dispersal model was formulated. A rearranged equation for freely falling bodies solves for time ($t_e = (h_e(2)/(1/g))^{1/2}$) allowing the calculation of a standardization multiplier ($x_e = t_e/t_e$) based on buoyancy. A calculation of "effective" plant height ($h_e = h_e(x_e)$) is substituted for actual height (h_a) in the equation above to calculate an "actual" time (t_a). Dispersal distance is calculated for selected wind speeds $x_d = (v_e)t_e$. This model accurately predicted seed dispersal distance in a laboratory experiment and supports seed dispersal in the field previously reported.

PRELIMINARY OBSERVATIONS OF THE
REPRODUCTIVE ECOLOGY OF
CYPRIPEDIUM FASCICULATUM. Richy J. Harrod and Dottie E. Knecht U.S.D.A Forest Service, Leavenworth, WA.

The reproductive ecology and biology of the rare *Cypripedium fasciculatum* was studied during the summer of 1993. Study sites were selected based on population size (>30 aerial stems) and accessibility. Evidence of autogamy and agamospermy were tested for through the use of pollinator exclusion bags. Treatments included bagging flowers and no further treatment, bagging and emasculating flowers, and bagging and hand-selfing flowers. Controls were tagged and not manipulated. Bagged, non-manipulated and bagged, emasculated plants produced no fruits. Fruits were produced on control and selfed plants, but there was no significant difference in number of seeds produced by either treatment (means of 3874 and 3356, respectively). Fruit production was 28% in control plants and 40% in selfed plants. A biotic vector is required for successful pollination and subsequent fruit and seed set. However, no insects were observed visiting this species. Determining the pollinator is important because future management of the species should include management of required pollinator(s).

LARVAL TAILED FROGS ALTER THEIR
FEEDING BEHAVIOR IN RESPONSE TO
NON-VISUAL CUES FROM FOUR AQUATIC
PREDATORS. Charles P. Hawkins, Utah State University, Logan, UT. Jack Feminella, Auburn University, Auburn, AL.

We used in-stream enclosures to examine whether chemical cues released by three predators affected feeding behavior of tailed frog tadpoles. In the presence of Giant Salamander- and trout-conditioned water, tadpoles reduced their feeding activity by 3-6 fold compared to predator-free controls. In contrast, tadpoles maintained high feeding activity in the presence of sculpin-conditioned water. Consumption experiments showed that natural densities of each predator species could potentially consume $> 50 / \text{m}^2 / \text{yr}$, far more tadpoles than produced in nature. These results suggest that *Ascaphus* may only be able to maintain high tadpole populations in streams either lacking predators or only containing predators that tadpoles can chemically sense.

PATTERNS OF ABUNDANCE AND
GROWTH OF TAILED FROG POPULATIONS
NEAR THE MT. ST. HELENS BLAST ZONE. Charles P. Hawkins, Utah State University, Logan, UT. Jack Feminella, Auburn University, Auburn, AL. Charles M. Crissafulli, Mt. St. Helens National Monument, Amboy, WA.

Data collected during the summers of 1985-1993 from 9 to 15 streams near Mt. St. Helens, WA revealed that abundance of tadpoles of *Ascaphus truei* varied strongly (0 to $21/\text{m}^2$) over space and time. Year of sampling explained more (36%) variation in abundance than did site (30%). Most of the annual variation in tadpole density was associated with magnitude (13%) and timing (11%) of discharge events that occurred prior to summer sampling (Nov. - Apr.). Most of the spatial variation in abundance was associated with differences among basins in temperature. Individual growth rates were highest in streams with maximum temperatures ca. 16°C . but tadpole production ($\text{g}/\text{m}^2/\text{yr}$) was highest in streams in which the riparian canopy had been removed by the eruption.

THE ROLE OF HYDRAULIC LIFT IN COMPETITION BETWEEN DEEP- AND SHALLOW-ROOTED GRASSES. Joseph L. Healy, S.O. Link* and R.A. Black. Washington State University, Pullman, WA 99163 and *Pacific Northwest Laboratory, Richland, WA 99352, USA.

Competition between root systems of neighboring plants may be altered by seasonal variation in precipitation and soil moisture. Competitive effects of a deep-rooted grass, *Pseudoroegneria spicata*, on a shallow-rooted grass, *Poa sandbergii*, were monitored by isolating the root system of *P. sandbergii* individuals within PVC tubes and comparing plant and soil characteristics to controls. When isolated for the entire growing season, *P. sandbergii* continued growth three weeks longer and late season soil water content was significantly greater than controls. Flowering phenology was unchanged. When plants were isolated late in the season, treated plants showed more negative predawn xylem pressure potential the morning after isolation. Compared to controls, soil water content was reduced the day after tube insertion. These effects on plant and soil water status may be due to removal of water supplied nightly by hydraulic lift. Research was funded by the US Department of Energy under contract DE-AC06-76RLO 1830.

EXPLORING PREDICTIVE MODELS FOR *CAMASSIA QUAMASH* PURSH (Greene) USING DATA FROM ECOLOGICAL PARAMETERS AND GEOGRAPHIC INFORMATION SYSTEMS. Thomas P. Henn, Central Washington University, Ellensburg.

Habitat analysis was combined with computer-aided spatial analysis to predict the occurrence of *Camassia quamash*, a traditional Native American food. Site and plant association data were gathered for 20 populations in Kittitas County. Primary on-site focus was ocular estimation of the percentage of ground cover for camas and the species growing with it. Ten quadrats of 1 square meter were sampled for 2 transects of 30 meters for each population. Transect data were interpreted using cluster and principal components analysis to examine similarities among plots and sites, and correlations of other variables with the presence of camas, respectively. G.I.S. were used to extract and analyze digital site data including, satellite image processing and georeferencing. Camas was found to correlate, with several species, including *Artemisia tripartita*, *Achillea millefolium* and *Perideridia gairdneri*. This species prefers open, seasonally wet, gently sloping areas.

TAXONOMIC STATUS OF *QUERCUS ACERIFOLIA* (FAGACEAE) AND A MORPHOLOGICAL COMPARISON OF FOUR MEMBERS OF THE *QUERCUS SHUMARDII* COMPLEX. William J. Hess, The Morton Arboretum, Lisle, IL and Nick Stoyanoff, Glenbard East High School, Lombard, IL.

Palmer (1927) described a "very distinct looking Oak" from the bluffs of Magazine Mountain, Arkansas and named it *Quercus shumardii* var. *acerifolia* in reference to its sugar maple-like leaf shape. We compare leaf and acorn morphology among the members of what we call the *Quercus shumardii* complex, namely: *Q. shumardii*, *Q. acerifolia*, *Q. texana*, and *Q. buckleyi*. The results of cluster analyses and discriminant function analyses are presented and support the recognition of the maple-leaf oak at the species level.

A RESEARCH TOOL TO AID COMPROMISE: WHAT SHOULD I MEASURE? Annette Hoffmann, Duane A. Neitzel, Pacific Northwest Laboratory, Richland, Aaron English, ASCL, Richland.

In fisheries research projects, one often desires to compare groups of fish. The basis for comparison is often a quantity that describes an attribute such as behavior, physiology, or morphometry. A question often arises, 'what is the best measure to use?' Several measures may be candidates for describing the attribute. The answer depends on the discriminatory properties of the candidate measures. To adequately contrast two groups, the comparison should be based on measures most likely to exhibit differences, i.e. measures sensitive to the treatments applied. As part of the Yakima Fisheries Project, we have developed a matrix that describes statistical properties of various measures made on spring chinook. The matrix can be used by research projects on spring chinook throughout the Pacific Northwest to help make compromises and decisions about which measurements to make when comparing groups of fish.

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USE OF NORTHWEST FOREST CANOPIES BY LARGE BIRDS. Scott P. Horton, Washington State Department of Natural Resources, Forks, WA.

Canopies of Pacific Northwest coniferous forests are diverse in composition, structure, context, and function. Among the functions provided by these canopies are nesting, roosting, or foraging habitat for 36 species of large birds (arbitrarily defined as not Passeriformes, Piciformes, or Apodiformes) of 11 families: Ardeidae, Anatidae, Cathartidae, Accipitridae, Falconidae, Phasianidae, Alcidae, Columbidae, Tytonidae, Strigidae, and Alcedinidae. Forest canopies are important at various parts of their life-cycles, as: foraging habitat (25/6, species/families), nesting habitat (30/8), and roosting habitat (30/9). Species of 3 families (Accipitridae, Columbidae, and Strigidae) use forest canopies throughout their lives. Canopy composition is especially important to Phasianidae, Columbidae, and some Strigidae; canopy structure and context (position of forests within the landscape) are important to all. Canopy composition is related to food availability for herbivorous birds, and to that and other elements of habitat for some strigids. Structural features important for foraging include canopy gaps, layering, and density; important features for nesting include cavities, support for platforms, and cover; structures important for roosting include canopy density, depth, and height. The juxtaposition of forests with appropriate canopies and other habitat elements is of primary importance to those birds that meet some of their life needs outside of forests.

A STUDY OF THE SUMMER STEELHEAD, *Oncorhynchus mykiss* IN SEVERAL INTERMITTENT TRIBUTARIES OF THE SATUS CREEK BASIN, WASHINGTON. Joel D. Hubble, Central Washington University, Ellensburg.

The summer steelhead, *Oncorhynchus mykiss* population was studied in three intermittent tributaries in the Satus Creek basin. The overall study goal was to further understand the life history pattern of the Satus Creek basin summer steelhead population and to contribute to the limited information base that exists for steelhead populations residing in intermittent streams. There was a strong tendency for post emergent fry, resulting from redds located in intermittent reaches to move downstream. However, survival to perennial flow conditions was very low. Steelhead production in Dry Creek (intermittent flow) appears to be lower than in Logy Creek (perennial flow), because of elevated water temperatures and minimal spring and summer stream flow. Electrophoretic analysis indicated that the Satus Creek basin steelhead populations are not distinguishable into genetic substocks.

LINKING LANDSCAPE PATTERNS TO AVIAN HABITAT RELATIONSHIPS Mark H. Huff, Pacific Northwest Research Stn. Olympia, WA, T. Kim Mellen and Rich Hagestedt, Mt. Hood/Gifford Pinchot National Forests. Gresham, OR.

Our objective was to develop an analysis procedure to predict vertebrate occurrence relative to landscape patterns. We modeled habitat relationships conceptually based on residency; distribution; home range; patch configuration; and suitability of moisture conditions, vegetation structure and composition, and special and unique habitats. We grouped bird and other vertebrate species occurring at Mt. Hood National Forest into 33 guilds by similar environment-use patterns. From this, we proposed general landscape configurations use for each guild. A spatial analysis model, LINKAGE ANALYSIS, was developed to predict suitability of individual patches and patch mosaics for different guilds. Suitability predictions provide a framework to establish monitoring protocol and validate habitat relationships.

METHODS AND MATERIALS UTILIZED IN THE CONSTRUCTION OF MINIMAL IMPACT RAINFOREST CANOPY ACCESS SYSTEMS Stephanie Hughes, Kevin Jordan, Arbonaut Access, Tofino B.C.

In this paper we discuss the history of canopy access for the purpose of research, and it's progression from tropical to temperate zones. The purpose of establishing Canopy Research Stations is to provide a safe base from which a wide application of research can be conducted, and to ensure that the study area is not being negatively impacted. Initial access is gained by a hand powered winch/pulley, and back-up safety system. All structures are strapped to the trunk; our system does not employ any intrusive methods such as nails or spurs. Ladders are installed with a running safety system to allow researchers to work at any level. Once in the canopy different trees in the system can be accessed by "burma bridges." Methods for initial access will also be discussed with emphasis on techniques developed specifically for minimal impact climbing.

NATURAL AND ARTIFICIAL DEN SITES USED ON THE FOREST ECOSYSTEM STUDY, FORT LEWIS, WA. David E. Johnson and Andrew B. Carey, USDA Forest Service, PNW Research Station, Olympia, WA.

In young, managed Douglas-fir (*Pseudotsuga menziesii*) forest on Fort Lewis, WA, an ecosystem management experiment is being conducted. A primary objective is to increase the prey of the northern spotted owl (*Strix occidentalis caurina*) by increasing den sites for northern flying squirrels (*Glaucomys sabrinus*). Natural den sites used by flying squirrels in these stands include stick nests, moss nests, cavities, stumps, snags, and downed logs and root wads. From December 91 to December 93 a total of 381 den sites were found. Thirty-two artificial cavities and nest boxes (1:1 ratio) have been installed in each of 8 stands (32 acres each). The first year 32 squirrels began using nest boxes. Artificial cavities have not been used yet. Full evaluation, and use, is not expected before late 1995.

PRELIMINARY EVALUATION OF ARTIFICIAL NEST BOXES AND CAVITIES IN MANAGED STANDS.

David E. Johnson and Andrew B. Carey, USDA Forest Service, PNW Research Station, Olympia, WA.

An ecosystem management experiment is being conducted in young, managed Douglas-fir (*Pseudotsuga menziesii*) forest on Fort Lewis, WA. A major goal of the experiment is to increase the availability of den sites for the primary prey of the northern spotted owl (*Strix occidentalis caurina*) by providing artificial cavities and nest boxes. One hundred and twenty-eight cavities and nest boxes at a density of greater than 1/acre were installed during spring, 1992. Upon first inspection (January 1993), the nest boxes yielded no live captures of any species. The second inspection (June 1993) found 32 northern flying squirrels (*Glaucomys sabrinus*), the primary target species, and 37 Douglas' squirrels (*Tamiasciurus douglasii*) in the nest boxes. In contrast, no squirrels have been found in the artificial cavities. Our specially designed boxes provide a more secure den site than cavities, and we expected them to be used first. However, high use of cavities was not expected before year three (1994), and formal evaluation is not planned until 1996.

THE YAKIMA RIVER CORRIDOR: HABITAT POTENTIAL AND LAND USE
Will Johnson, Graduate Student,
Central Washington University,
Ellensburg, WA

POSTER SESSION: Maps and photos indicate how approved land use has altered the habitat potential of the Yakima River corridor. More than 600 house lots have already been approved in one twelve-mile segment of the river and adjacent flood plain. This form of development has and will continue to have important negative impacts on critical habitat components; e.g. river hydrology, water quality, wetlands, soils, vegetation, shade and cover. Cumulative effects on public safety and the ecosystem are not given full consideration in the political decision-making process.

REPTILES OF THE PACIFIC NORTHWEST.

Lawrence L. C. Jones, USDA Forest Service, Pacific Northwest Research Station, Olympia, Washington, and William P. Leonard, Department of Ecology, Olympia, Washington.

The reptile fauna of the Pacific Northwest is relatively meager (30 species in Washington, Oregon, and Idaho) when compared to the more xeric southern temperate and tropical climes. Only about four species are considered typical of the Pacific Northwest (2 lizards and 2 snakes). The cool, maritime climate west of the Cascades is home to only a few species, and only one, the Northwestern Garter Snake, is broadly endemic to this area. Most of the diversity occurs in the warmer, more xeric areas east of the Cascades, where activity periods for dry-adapted ectotherms can be relatively long. Diversity also increases with decreased elevation and latitude; hence, the most speciose region is southeastern Oregon and southern Idaho, where several true desert species meet their peripheral northern range. Several species typical of areas to the south have restricted ranges or disjunct populations in the Northwest, including the California Mountain King Snake, Common King Snake, Mojave Black-collared Lizard, and all turtles. In this display, we will show a sample of live reptile species native to the Northwest.

ECOLOGY OF AMERICAN MARTENS IN A LODGEPOLE PINE-BITTERBRUSH COMMUNITY IN SOUTH-CENTRAL OREGON: AN EARLY PROGRESS REPORT. Lawrence L. C. Jones and Martin G. Raphael, USDA Forest Service, Pacific Northwest Research Station, Olympia, Washington.

Since early May 1993, we have radio-collared 25 martens (20 males, 5 females) in south-central Oregon, near the town of Chemult, east of the Cascade crest. The habitat is predominately a lodgepole pine-bitterbrush community, but inclusions of ponderosa pine and white pine occur at prominent topographic features and at higher elevations. We obtained a total of 663 locations of martens using ground-based telemetry. Preliminary home range estimates (minimum convex polygon) show that male martens ($n = 10$; animals with > 25 locations) average about 745 ha and females ($n = 2$) average 302 ha. We have described 63 different resting sites; most (67%) are slash piles resulting from road construction or timber harvest activities. Other resting sites include logs (11%), standing dead trees (10%), and rootwads (2%). Ponderosa pine accounted for 60% of the tree, snag, and log species, although lodgepole pine dominates the landscape. Diameters for live tree, snag, and log resting sites were 73.0, 84.5, and 36.1 cm, respectively. All five maternal dens sites were in large live or standing dead trees.

REMOTE PHOTOGRAPHIC TECHNIQUES FOR DETECTING AND MONITORING CARNIVOROUS MAMMALS. Lawrence L. C. Jones and Martin G. Raphael, USDA Forest Service, Pacific Northwest Research Station, Olympia, Washington.

Remote-automated photography can be a powerful tool for biologists studying carnivores. Cameras may be used to detect the presence or relative abundance of certain species. Habitats and management areas can be surveyed for presence (but not necessarily absence) of target species. Cameras vary greatly in cost and effectiveness. In general, the more expensive and technologically advanced a system is, the more productive the output. Other devices may be more efficient for detection, but cameras offer indisputable proof of the occurrence of target species. In addition, cameras are important tools for learning behavioral characteristics. We have successfully used inexpensive 110 cameras with mechanical triggers to detect martens in our western Washington Cascades study area for the purpose of radio-collaring. In our study area in the eastern Cascades of Oregon, we have monitored maternal den sites of martens using video cameras and 35-mm SLR cameras with infrared monitors as triggers. Five types of camera systems are displayed, along with photographs and video footage of a marten den and martens and fishers at bait stations.

HABITAT CHARACTERISTICS OF MULE DEER BEDSITES IN GRANT AND DOUGLAS COUNTIES, CENTRAL WASHINGTON. Brian E. Kelley, Ecologist, U.S. Forest Service, Colville, WA.

Wild ungulates primarily select bedsites for thermoregulatory and security cover benefits. These benefits are critical for females who have higher energetic demands during gestation and lactation and who face the added risk of predation on their offspring. Information describing this component of deer cover can improve management and conservation of important habitat. Structural and topological bedsite characteristics of female Rocky Mountain mule deer (*Odocoileus hemionus*) were examined from May-August, 1990 by comparing bedsites and random sites from six study areas. Deer exhibited preference for the mesic tree/shrub, giant wildrye, and irrigated Conservation Reserve Program (CRP) vegetation types. Stepwise analysis indicated percent screening cover, cover height, and distance to free water were the best discriminators between the two data sets. A linear model was then developed based on these variables using discriminant function analysis. The model correctly classified 93% of the bedsites from an independent data set collected from eight radio-collared deer. Results indicate the importance of these preferred sites in fulfilling the critical physiological and security requirements for female mule deer during summer on the semi-arid Columbia Plateau.

RESPONSES OF HEADWATER STREAM AMPHIBIANS TO FOREST PRACTICES IN WESTERN WASHINGTON. Kathryn A. Kelsey, College of Forest Resources, University of Washington, Seattle, WA 98195

Tailed frog tadpoles (*Ascaphus truei*) and Pacific giant salamander larvae (*Dicamptodon tenebrosus*) were sampled in eleven low order streams in western Washington managed forests during 1992 and 1993. In each stream, three 10m sections were randomly selected for amphibian searches. Rock and wood were removed to enable the capture of most amphibians within the 10m search area. Habitat characteristics of each stream were measured at ten transects along a 300m reach of stream. Correlations of amphibian abundance, density, and biomass to habitat characteristics reveal threshold levels of large organic debris necessary for sizeable populations of stream amphibians. In addition, presence of cobbles and boulders indicate habitat suitable for amphibians. At sites surveyed one year after timber harvest, stream amphibians were present in numbers comparable to pre-harvest levels, indicating that amphibians were able to survive the actual logging operations. More data are needed to assess the impacts of changing environmental conditions to stream amphibians and stream habitat after timber harvest.

A STUDY OF THE HABITAT CHARACTERISTICS OF THE SPOTTED SKUNK, *SPILOGALE PUTORIUS*, IN WESTERN WASHINGTON AND OREGON. Janet E. Kershner and Andrew B. Carey. USDA Forest Service, Pacific Northwest Research Station, Olympia WA.

During 1986-1989, surveys of young, mature, and old growth forests, we caught 189 spotted skunks, *Spilogale putorius*. In the Oregon Coast Range, 144 captures were recorded. Of these 123 (85%) were recorded in eight old growth, 7 (5%) in three naturally mature, and 14 (10%) in nine young, managed stands. Surveys on the Olympic Peninsula recorded 45 captures. Of these, 21 (46.5%) were recorded in five old-growth stands, 3 (7%) in two naturally mature stands, and 21 (46.5%) in seven young, managed stands. Results indicate significant differences in captures among stand conditions in the Oregon Coast Range ($p=0.0424$), but not in the Olympic Peninsula ($p=0.5405$). The only significant difference noted in captures between provinces was in young, managed stands ($p=0.0168$). Preliminary analysis using multiple regression identified some structural and vegetative features that accounted for 68-77% of the variation in captures within the province. These include characteristics such as number of medium snags and large conifers, and prevalence of ericaceous shrub cover.

VEGETATIVE CHARACTERISTICS CONTRIBUTING TO THE PRESENCE OF NORTHERN FLYING SQUIRRELS IN THE OREGON COAST RANGE. Janet E. Kershner and Andrew B. Carey. USDA Forest Service, Pacific Northwest Research Station, Olympia, WA 98512.

As part of a study in the Oregon Coast Range, we measured vegetation plots at 1790 trap stations in 8 old-growth, 3 naturally mature, and 9 young, managed stands. From this, we attempted to explain the number of individual Northern flying squirrels (*Glaucomys sabrinus*) using trap stations by the composition and structure of the vegetation at the stations. Levels of analysis that were conducted includes (1) microhabitat - using individual trap stations; (2) macrohabitat - among stations; and (3) stand condition - between stands. Previous work indicated that there is a significant difference in the density and capture estimates between natural and managed stand conditions. Preliminary results of multiple regression analyses indicated approximately 3-5 trap site characteristics could explain up to 70% of the variation in the numbers of flying squirrels. From this information, models were created that included combinations of compositional and structural features influencing flying squirrels presence.

A FIRE HISTORY OF THE BULL RUN WATERSHED. Fred Krusemark and James K. Agee, University of Washington, Seattle.

Past disturbance processes have created and defined what we call "natural" landscapes. Before we can manage these areas for the purpose of maintaining their natural state, we must first have some knowledge of the disturbance regime—frequency, intensity, magnitude, and type of disturbance—that formed the present landscape. To determine the past fire regime for a 27,000 ha watershed, tree cores, ring counts of stumps, and stump wedge samples were taken. Establishment dates of Douglas-fir (*Pseudotsuga menziesii*), fire scars, and presence of charred bark on residuals are being used to determine fire frequency. Fire boundaries will be delineated and the resulting fire maps will be used to create a GIS layer that can be used to separate fire regimes by vegetation association and subdrainage. Preliminary results indicate that stand ages range primarily between 80 and 750 years-old. The landscape seems to be dominated by large, low-frequency, high-severity fires; however, some sites were prone to repeated, low-severity fires resulting in several age-classes of Douglas-fir.

DISTURBANCE EFFECTS ON UNDERSTORY SPECIES OF A *PINUS PONDEROSA*-*PSEUDOTSUGA MENZIESII* FOREST. Ellen Kuhlmann, Rich Fonda, Western Washington University, Bellingham WA.

This study was designed to study effects of low intensity fire, select-cut harvest, and time postdisturbance on understory species in a *P. ponderosa*-*P. menziesii* community in North Central Washington. Data was collected on species presence and percent cover, seedling number, canopy cover, tree composition and abundance, and fuel loads on sites in the following groups: Fire5, Fire10, Harvest5, Harvest10, and Undisturbed. There was significantly greater species number in Fire5 than in Undisturbed, no other differences among disturbance type or time since disturbance was seen. No significant difference was found in total percent cover or graminoid, forb, or shrub cover for fire, harvest and undisturbed disturbance groups. 10 year postdisturbance plots had significantly more graminoid cover than 5 year plots. Fire5 and Harvest5 had significantly greater richness than Undisturbed. No significant differences in the diversity or evenness indices were found. Results suggest understory composition and cover are not principally controlled by source of disturbance in this *P. ponderosa*-*P. menziesii* forest.

COMPARING GROWTH OF DOUGLAS-FIR (*PSEUDOTSUGA MENZIESII* [MIRB.] FRANCO) AND RED ALDER (*ALNUS RUBRA* BONG.) IN A MIXED CLUSTER PLANTATION WITH STANDARD GRID PLANTATIONS. D.P. Lavender, W.H. Emmingham, Oregon State University, Corvallis.

In the spring of 1979, 2-0 Douglas-fir seedlings were planted in two configurations in a plantation five miles north of Corvallis, Oregon. 1. Grid--eleven rows of eleven seedlings each spaced eight feet between and within the rows, 2. Cluster--five seedlings, equally spaced on the circumference of circles six feet in diameter and spaced twenty-five feet apart on the cluster centers. Each plot contained eleven rows of eleven clusters each. In the spring of 1986, the clusters were thinned to three saplings per cluster and one-year-old red alder seedlings were planted in the center of the squares formed by four adjacent clusters. In the winter of 1994, the cluster planted Douglas-fir averaged 42 feet in height, 7.6 inches in diameter, and each tree had about thirty percent greater volume than the average of the saplings planted in the grid. The alder averaged 29 feet in height, 3.9 inches in diameter, and had a survival of 87%.

GRADIENT ANALYSIS OF THE VEGETATION IN A LAGOONAL SALT MARSH, WHIDBEY ISLAND, WASHINGTON. Emily Lefstad and Rich Fonda, Western Washington University, Bellingham.

Lake Hancock on Whidbey Island, Washington, supports a 69 ha salt marsh. North of California, marshes of this type are rare and usually <30 ha. The Lake Hancock environment is unique among marshes of the north Pacific coast. The marsh supports a single community dominated by *Salicornia virginica*, with *Triglochin maritimum*, *Distichlis spicata*, *Jaumea carnosa*, and *Atriplex patula* var. *hastata*. Environmental factors that most influence the vegetation pattern are elevation, distance from the inlet, and soil moisture. Both the environment and vegetation of the Lake Hancock marsh are more similar to the marshes of central and southern California than to the marshes of Oregon, Washington, British Columbia, and Alaska.

INTERPRETING HABITAT CHARACTERISTICS OF BIRDS AT STAND AND LANDSCAPE SCALES. John F. Lehmkuhl, Pacific Northwest Research Station, USDA Forest Service, Olympia, Washington.

I used sample data on birds from 148 stands of young to old-growth Douglas-fir forest in western Oregon and Washington, and landscape data around those stands to ask the question, "How do (1) stand environment, area, and shape, (2) the composition of the immediate stand neighborhood, and (3) the landscape composition and pattern affect the richness and abundance of birds in sampled stands?" Birds were sampled by point counts. Forest stands were mapped by age classes in a 2025-ha area around the center of the stands sampled for vertebrates. Few species showed thresholds of occurrence related to stand area ($R < 0.26$) with log-linear functions. Species richness was most strongly influenced by the stand location or environment, such as elevation, slope, or vegetation, rather than landscape variables in a multiple regression model. Ordination of species abundances showed that stand environmental attributes explained 32% of the variation in bird abundances, whereas landscape variables explained 15% of the variation. The relatively small influence of landscape variables may be the result of relatively low fragmentation in study areas, the dynamic nature of western forest fragmentation, lag effects in population responses, or lack of data on species most likely affected by forest fragmentation. The primary landscape gradient affecting bird abundances was correlated with the contagion pattern index and late-successional forest area and isolation around stands. A secondary gradient was associated with the fractal landscape edge index and old-growth area.

WESTERN LONG-TOED SALAMANDER DEMOGRAPHICS AND OVIPOSITION IN A SMALL VERNAL WETLAND OF THE PUGET SOUND LOWLANDS. William P. Leonard, Washington Department of Ecology, Olympia; Klaus O. Richter, King County Environmental Division.

Between 12 December 1993 and 30 January 1994, the demography and oviposition of the Western Long-toed salamander (*Ambystoma macrodactylum macrodactylum*) was studied in a 0.03 acre vernal wetland in Thurston County, Washington. Over 32 trapping nights, we captured 220 different salamanders (44 females and 178 males) in 20 aquatic funnel traps; marked adults were captured on 179 occasions. Only one capture was made during daylight hours indicating that these animals are highly nocturnal. We found 180 egg "masses" deposited in water ranging between 5 and 38 cm; 97% of the egg deposition sites were in water less than 25 cm in depth; all eggs were attached within 15 cm of the waters surface. Eggs were attached either to thin-stemmed emergent plants or small-diameter woody debris. The results suggest that small, shallow ponds containing thin-stemmed emergent vegetation and small diameter woody debris are productive for Western Long-toed Salamander reproduction.

THE ROLE OF FUNGI, LICHENS, AND BRYOPHYTES IN THE DEVELOPMENT OF MANAGEMENT ALTERNATIVES FOR FEDERAL LANDS IN THE PACIFIC NORTHWEST. Robin D. Leshner, U.S. Forest Service, Mountlake Terrace, WA, Roger Rosentreter, Bureau of Land Management, Boise, ID, John Christy, Oregon Natural Heritage Program, Portland, OR.

Federal laws and policy direct federal agencies to provide for biological diversity and viability of species in the management of public lands. Until recently, the primary emphasis has been on vertebrate species. Directed by court order, the USFS addressed viability of all species closely associated with old-growth forests. Lists were developed of old-growth associated species and used by the Scientific Analysis Team (1992) in evaluating effects of various alternatives on species viability. This process was expanded considerably for the development of the President's Forest Plan (FEMAT 1993). Many knowledgeable people provided information in this process. These groups of organisms represented 72% of all species evaluated, and included 527 fungi, 157 lichens and 106 bryophytes. To date, this was the most extensive viability analysis to be conducted, and was instrumental in refining management alternatives to provide for the viability of these species.

THE INFLUENCE OF HABITAT DEGRADATION ON THE BREEDING ECOLOGY OF LOGGERHEAD SHRIKES *LANIUS LUDOVICIANUS* IN THE SHRUBSTEPPE REGION. Matthias Leu and David A. Manuwal, University of Washington, Seattle.

Populations of Loggerhead Shrikes are decreasing at an alarming rate throughout the US. Little is known about the breeding ecology of the Loggerhead Shrike in the shrubsteppe region. In addition, shrubsteppe plant communities are undergoing drastic changes in species composition through the introduction of Eurasian grass species and intensive grazing. We are currently investigating the influence of degraded habitat found in the Yakima Training Center on the breeding success of Loggerhead Shrikes. We measured breeding success, fledgling survival, juvenile dispersal movements and nest-site selection. Of 36 nests, 58.3% were built in sagebrush (*Artemisia tridentata*) and 16.7% (n=36) nests were depredated during the incubation and nestling stages. The survival rate of juveniles prior to dispersal from the breeding territories varied from 29 to 100 %. Juveniles stayed anywhere from 4 to 74 days on the parental territory after reaching independence in clutches initiated during the month of April.

EFFECTS OF COPPICE DUNE TOPOGRAPHY AND VEGETATION ON SOIL WATER DYNAMICS IN A COLD-DESERT ECOSYSTEM. Steven O. Link, Pacific Northwest Laboratory, William J. Waugh, CNES Geotech, Grand Junction, Janelle L. Downs, Michael E. Thiede, Pacific Northwest Laboratory, James C. Chatters, Richland, Glendon W. Gee, Pacific Northwest Laboratory, Richland.

Relationships between coppice dune - swale topography and soil water dynamics were examined under normal and enhanced precipitation. The site is made up of coppice dunes dominated by Grayia spinosa, sparsely vegetated swales, and swales dominated by Artemisia tridentata. Topography and vegetational patterns were related to patterns in soil water storage and soil water content with depth. Sparsely vegetated swales were wetter than G. spinosa coppice dunes or A. tridentata swales. The effect of enhanced precipitation on end-of-season soil water storage was negligible. This work was supported by the U.S. Department of Energy under Contract DE-AC06-76RLO 1830.

SCALE DEPENDENT ANALYSES OF HABITAT SELECTION BY MARTEN IN THE SUB-BOREAL SPRUCE BIOGEOCLIMATIC ZONE, BRITISH COLUMBIA. Eric C. Lofroth, B.C. Ministry of Environment, Lands and Parks, Wildlife Branch, Victoria and Simon Fraser University, Burnaby.

Winter habitat selection by radio-collared marten (*Martes americana*) was examined at landscape, stand and patch scales between January 1988 and September 1991. Landscape scale analyses for 7 adult marten (4 males, 3 females) revealed that marten preferentially included mature to old growth seral stage habitat types of mesic to hygric moisture regimes within home ranges. Three male marten included substantial areas of young forest seral stage habitat types which may provide access to alternate prey during periods of high prey population cycles. Stand scale analyses indicated that marten did not prefer particular habitat types but avoided some habitat types, particularly young seral stages, xeric habitat types and wetlands. Marten exhibited selectivity at the stand scale for habitats types classified by their structural features. These habitat preferences were related to the abundance of coarse woody debris, deciduous canopy closure, high shrub and low shrub closure, and abundance and size of trees and snags. At a patch scale, marten selected sites where structural characteristics were significantly different from the prevailing characteristics of the habitat types the sites were in.

CHRONOLOGY OF CIRQUE MORAINES BETWEEN MOUNT STUART AND BONANZA PEAK, NORTH CASCADE RANGE, WA.

William A. Long, 123 Riverfront Drive, Cashmere.

The purpose of this study was to establish a chronology of cirque moraines in the North Cascades between Mount Stuart and Bonanza Peak, the two highest nonvolcanic peaks in the Cascade Range. Dendrochronology, tephrochronology and relative position were used in dating the moraines. In many cirques are two belts of moraines: outer moraines are pre-Mazama and inner moraines are late-Neoglacial in age. Many weathered cirque moraines are overlain by the ca. 7000-yr-old Mazama ash as well as the 11,250-yr-old Glacier Peak pumiceous tephra and thought to date from latest Pleistocene time, and fresh moraines are ash free and dated from the middle 19th century by dendrochronology. In 35 cirques moraines are Mazama ash mantled and in 10 cirques moraines are mantled by both Mazama and Glacier Peak ashes, implying that these moraines possibly comprise two glacial readvances -- one latest Pleistocene and the other early Holocene in age. As only a minimum limiting age is available for the pre-Mazama cirque moraines, rather than early Holocene, they could represent a last-glacial episode of advance.

ESTABLISHMENT OF CONIFERS UNDER EXISTING RIPARIAN VEGETATION IN THE OREGON COAST RANGE. Kathleen Maas, William Emmingham. Adaptive COPE, Oregon State University, Newport.

Past logging practices and fires have resulted in red alder dominated riparian areas. Six sites have been established to evaluate the species and vegetation manipulations best suited for conifer reestablishment. Four conifer species (Douglas-fir, grand fir, western hemlock, and western redcedar) were planted with and without tubing in 1989 under three overstory treatments (control, 50% girdled, and 100% girdled), two understory treatments (weed control first year and no control). After three years of growth, survival appears highest with 50% girdled overstory (72%), vegetation control (71%). Western redcedar had the highest survival (73%) while Douglas-fir was the lowest (52%). Relative tree growth benefited most from 100% girdled overstory and vegetation control. Western hemlock had the highest relative basal diameter growth and relative height growth. Tubing was not a significant factor for survival or growth.

WHERE WE CAME FROM AND WHAT'S NEXT FROM A HISTORICAL PERSPECTIVE. David B. Marshall, Consulting Wildlife Biologist, Portland, OR.

A review of American ornithological journals for this century indicates concepts and methodologies used in landscape ecology did not appear until the early 1970s. Prior to that time papers centered on taxonomy and morphology, anatomy and physiology, distribution, life histories, biology, food habits, behavior, and eventually energetics. Aldo Leopold introduced the concept of carrying capacity in the 1930s, but it was not put into practice until many years later. Even by the 1950s, habitat studies were few and ecological concepts were in their infancy. Data quantification, statistical sampling, home range and telemetry, the island biogeography theory and population modeling represent recent advances. However, these disciplines are dependant upon continued investigations in the fields covered before 1970. The Bureau of Biological Survey, an agency that evolved into the U.S. Fish and Wildlife Service, began with the same mission as Secretary Babbitt's new agency, the National Biological Survey. The old agency did not get to finish its job. Without basic information on taxonomy, distribution, demographics, and life histories, modeling and other tools used in population studies, landscape ecology and ecosystem management cannot be effective. Our educational and political system is not conducive to an ecological approach, but supports species management. Where we go from here demands more information on many of the old disciplines and a new approach to organization of conservation agencies.

EVALUATION OF WATER SOURCES FOR THE ARTIFICIAL PRODUCTION OF ANADROMOUS SALMONIDS. Gregg A Martenson and Dennis Dauble, Pacific Northwest Laboratory, Richland, Washington.

Several fish production facilities, including acclimation sites may be constructed in the Yakima River basin for the Yakima Fisheries Project (YFP). The objective of our studies was to evaluate the suitability of water supplies at these locations for use in fish culture activities. Live boxes with pre-smolt fall chinook salmon (*Oncorhynchus tshawytscha*) or rainbow trout (*O. mykiss*) were used for *in situ* evaluations of surface water. Egg incubation bioassays were used to determine if groundwater from the YFP sites could be used for rearing salmonids during early life stages. Plasma cholesterol and protein levels of live box fish were affected by diet and other environmental conditions, while leucocrit and glucose were fair indicators of acute stress. Egg incubation results indicated no difference in the survival, growth, or anomalies of rainbow trout embryos among the four groundwater sources and reference controls. Live box studies were not effective for comparing the response of fish to surface water conditions because natural fluctuations in temperature and flow occurred at the different sites. However, the egg incubation studies were effective for screening water sources used to culture early life stages of salmonids.

VARIATION IN RAINBOW TROUT POPULATIONS OF THE UPPER YAKIMA RIVER: IMPLICATIONS FOR ECOLOGICAL IMPACT ASSESSMENT. Steven W. Martin and Todd N. Pearsons, Washington Department Wildlife, Ellensburg.

The density of salmonid fishes in streams shows great natural variability in time and space making assessment of impacts to a population difficult. Rainbow trout densities and distribution have been monitored by electrofishing in tributaries of the upper Yakima River annually since 1990. Results have shown that the distribution of rainbow trout has remained relatively constant through time but that density has been highly variable in both time and space. Although spatial variability is high it may be partially explained by the following five physical habitat variables: habitat complexity, site elevation, site width, amount of pool area, and discharge. In contrast, temporal variation of rainbow trout densities is not as well understood. The coefficient of variation of population size may be a useful tool for quantifying temporal population stability resulting in better designs of ecological impact assessment studies.

BRANCH SAPFLOW MEASUREMENT AS A TOOL FOR INVESTIGATION OF CANOPY PROCESSES IN *ABIES AMABILIS*. T.A. Martin, K.J. Brown, T.M. Hinckley, J.S. Rombold, University of Washington, Seattle, F.G. Meinzer, Hawaiian Sugar Planters Association, Aiea, Hawaii, J. Cermák, J. Kucera, University of Agriculture, Brno-Sobesice, Czech Republic, R. Ceulemans, University of Antwerp, Wilrijk, Belgium.

For approximately ten weeks during summer 1993, we measured sapflow of seven Pacific silver fir (*Abies amabilis*) branches with a non-invasive heat-balance technique. The extensive temporal coverage of this data allowed us to investigate several topics: 1) Diurnal patterns of water use of *A. amabilis* branches 2) The relationship between branch sapflow and environmental variables 3) The presence of nighttime stomatal opening 4) The degree of coupling of *A. amabilis* foliage to the atmosphere 5) The use of branches as units of integration for canopy-level estimates of water use and stomatal conductance.

FIRE FREQUENCY SURVEY IN THE BLUE MOUNTAINS, OREGON AND WASHINGTON. Kathleen R. Maruoka, University of Washington, Seattle, WA.

Fire occurrences were documented at fifteen sites in the Blue Mountains. Sites were selected based on vegetation association and the presence of fire-scarred trees. Vegetation associations ranged from *Pseudotsuga menziesii* to dry *Abies grandis*. Slope, aspect, and elevation varied between sites. Fire frequencies were based on samples from fire-scarred trees. Mean fire return intervals ranged from 9.9 to 49.0 years, with sample standard errors from 4.8 to 41.6 years. Mean fire return intervals and associated sample standard errors were qualitatively compared between sites based on slope, aspect, elevation, relative geographic position, and vegetation association. Fire frequency and frequency variability could not be linked between sites to physical, geographic, or floristic gradients.

DWARF MISTLETOES IN FOREST CANOPIES. Robert L. Mathiasen, Idaho Department of Lands, Coeur d'Alene.

Dwarf mistletoes (*Arceuthobium* spp.) are parasitic flowering plants found throughout much of western North America parasitizing members of the Pinaceae. Heavy infection by these parasites affects biomass distribution on individual trees and hence within forest canopies. Most dwarf mistletoes induce the formation of witches' brooms on infected hosts and these brooms can significantly alter the structure of forest canopies as well. Conversely, forest canopy structure greatly affects spread and intensification of dwarf mistletoes. Dwarf mistletoes interact with other organisms that also inhabit forest canopies, such as birds, mammals, insects, and fungi. The principal interaction involves the mistletoes as a food source for these organisms, but birds and mammals also use witches' brooms as nesting and foraging sites. Another interaction involves long range dissemination of dwarf mistletoe seeds by animal vectors, primarily birds and squirrels.

A NEW SPECIES OF *ACHNATHERUM* (*ORYZOPSIS*) FROM OREGON. Jack Maze Department of Botany, University of British Columbia, Vancouver, B. C. V6T 1Z4 and Kathleen A. Robson, Rare Plant Consortium, Department of Biology, Central Washington University, Ellensburg, WA 98926.

A new species of *Achnatherum*, *A. wallowaensis* Maze et K. A. Robson, from central and northeastern Oregon is described. It is closely related to *A. hendersonii* (Vasey) Barkworth (= *Oryzopsis hendersonii*) of central Washington and Oregon but differs most obviously in its lax inflorescence with drooping spikelets; *A. hendersonii* has stiff inflorescences with erect spikelets. These plants differ also in spikelet and vegetative traits as revealed by principal components analysis. Like *A. hendersonii*, *A. wallowaensis* occurs as relatively small populations in disjunct areas of shallow, rocky soils that support a vegetation of small, distantly spaced plants. The restricted distribution of *A. wallowaensis* renders it sensitive to disturbance. Its segregation from *A. hendersonii* considerably reduces the number of populations of that species placing it in similar jeopardy.

SPOROPHYTE PRODUCTION AND INVERTEBRATE POPULATION FLUCTUATIONS IN *SCHISTIDIUM MARITIMUM* (TURN.) BRUSCH. & SCHIMP, YACHATS, OREGON. Kathy Merrifield, OSU Botany and Plant Pathology, Corvallis, OR 97331-2902.

Ten randomly selected clumps of *Schistidium maritimum* were removed from coastal splash zone basalt at Yachats, Lincoln County, Oregon each month from February 1993 through January 1994. *Eudorylaimus* sp., an omnivorous nematode, and *Ameronathrus* sp., an algal-feeding mite, were extracted using a modified Baermann funnel method. Additional *Ameronathrus* sp. emerged on air-dried sample surfaces. *Eudorylaimus* sp. and *Ameronathrus* sp. as well as *S. maritima* perichaetia, mature sporophytes, and post-mature sporophytes per gram of air-dried moss were calculated. Perichaetia exceeded 60/g from August through October and were markedly lower in other months. Mature sporophyte production peaked at 15.2/g in November, declined gradually through January, and was less than one during the rest of the year. Few post-mature sporophytes were found. *Eudorylaimus* sp. populations of 45.6 in February declined steadily through spring and remained low through summer and fall except for an isolated August peak; a late fall increase culminated in a December peak of 59.7/g. *Ameronathrus* sp. population peaks of 9.9 in May and 12.9 in September contrasted with levels of usually 5.0/g or less during the remainder of the year. *Eudorylaimus* sp. populations were lowest during most of the drier months, while *Ameronathrus* sp. populations were highest during much of the dry season. The mature sporophyte production peak one month before the highest *Eudorylaimus* sp. peak suggests the possible use of moss spores as a nematode food source. No other invertebrates were found throughout the study.

WATERBIRD CENSUSES OF CABELL MARSH, 1992 AND 1993. Kathy Merrifield, OSU Botany and Plant Pathology, Corvallis OR, 97331-2902, and Maura Naughton, Finley National Wildlife Refuge, 26208 Finley Refuge Rd., Corvallis, OR 97333.

Between late April and late October of 1992 and 1993, KM conducted 14 and 20 waterbird censuses, respectively, at Cabell Marsh, Finley National Wildlife Refuge, Benton County, in Oregon's Willamette Valley. In 1992, the seventh year of drought, the water level was low, exposing extensive mudflats. In 1993, after heavy winter precipitation, higher water covered bare mud and inundated most emergents. Pied-billed grebes, wood ducks, mallards, and American coots, all breeding species, were more abundant during 1993 than in 1992, and hatch year birds were seen more frequently, in higher numbers, and later in summer during 1993. In contrast, more cinnamon teal, also a breeding species, were observed during 1993. Numbers of great blue herons, solitary breeders within the refuge, were similar over the two years but were highest in spring and fall of 1992. Among post-breeding migrants, great egret, killdeer, and greater yellowlegs were more abundant in 1992 than in 1993, and western, least, and pectoral sandpipers were observed during 1992 only. Numbers of northern pintail and of green-winged teal, both wintering species, were similar during both years. The higher water level in 1993 appeared to enhance food and cover production and/or availability for most breeding species but to decrease resource access for post-breeding migrants.

A TAXONOMIC KEY FOR WASHINGTON STONEFLY NYMPHS USING HYPERCARD. Noboru Minakawa, University of Washington, Seattle, Gerald F. Kraft, Western Washington University, Bellingham.

This program keys stoneflies to family and genus, and also acts as a database. It was developed with HyperCard for Macintosh. Users operate this key with graphics and short written descriptions. A main screen (card) shows several nymphal characteristics with images and short descriptions. Using a mouse pointer to select appropriate images for a working specimen results in the elimination of unmatched taxa. Users may select from any displayed characteristics, so experienced workers may identify a taxon with fewer steps. The process is quite fast and easy since all choices are on one card. Selected characteristics are highlighted so that users can keep track of their choices. After a wrong selection an operator can deselect and make a new selection, or start over from the beginning with one command. When the number of possibilities reaches one, the program displays the name, description, and figure of the found taxon. With this program, relatively unskilled workers identify nymphs efficiently, and their learning about insects is reinforced. Keys may be created for other groups by substituting information in the program.

STUMP SPROUTING IN PACIFIC YEW.
Don Minore, Pacific Northwest Research
 Station, Corvallis, OR.

Stump characteristics and overstory canopy were related to the initiation and survival of epicormic branches (sprouts) on Pacific yew stumps to monitor and assess asexual reproduction in harvested yew stands. One hundred yew stumps were measured in each of 11 recently harvested stands during 1992 to determine stump characteristics, initial sprouting, and overstory canopy density. Half of those stumps were artificially shaded. All of them were remeasured in 1993. The number of sprouting stumps in each stand was well correlated with average stump height and average bark retained ($R^2 = 0.93$). Postharvest sprouting was most abundant on stumps with established sprouts or branches. For individual stumps, the number and length of preharvest sprouts were the only variables consistently related to number of postharvest sprouts. Artificial shading was detrimental.

EVOLUTIONARY IMPLICATIONS OF RBCL
 SEQUENCE VARIATION IN ROSACEAE.
David R. Morgan, Western Washington
 University, Bellingham. Douglas E. Soltis,
 Washington State University, Pullman.

Phylogenetic analysis of sequences of the chloroplast gene *rbcl* in Rosaceae was performed to address evolutionary problems posed by the family. Analyses of *rbcl* sequence data delineate groups of genera within Rosaceae comparable to subfamilies Maloideae, Prunoideae, and Rosoideae, although the composition of each group differs from traditional circumscriptions. The pome-fruited Maloideae include the capsular and follicular-fruited genera *Vauquelinia*, *Lindleya*, and *Kageneckia*, and all members of Rosoideae with chromosome numbers of $x = 9$ are separated from the $x = 8$ and 7 members of the subfamily. In addition, Spiraeoideae are not monophyletic. When considered with data from secondary chemicals, floral anatomy, and rust parasites, *rbcl* evidence suggests that chromosome numbers are more reliable indicators of generic alliances than the more commonly used fruit types. Molecular data are consistent with some traditionally held views of evolution of chromosome numbers and fruit types, but suggest that achenes have been derived at least five times. This study also suggests that the subfamily Maloideae has been derived from spiraeoid ancestors and that pome fruits are derived from follicles or capsules.

PREHISTORIC UTILIZATION ON THE
 COLUMBIA PLATEAU. Vera Morgan,
 Archaeological and Historical Services, Eastern
 Washington University, Cheney.

Archaeological records indicate that Native Americans have exploited resources within the Columbia Plateau for at least 11,000 years. Big game hunting (including now extinct species) was supplemented by fishing and food gathering until about 6000 years BP. Climatic changes, beginning about 8000 years BP and reflecting drier conditions, are thought to be a major contributor to succeeding changes in subsistence strategies. Economic adaptations after 6000 years BP include a more efficient exploitation of fish, small game, and plant foods coupled with increased sedentism. Between 2500 and 2000 years BP, subsistence is marked by a sophisticated exploitation of the natural environment accompanied by attendant shifts in seasonality, scheduling, and settlement patterns. Population expansion is evidenced by a larger number of riverine and specialized upland sites and increased riverine village size. The ethnographic to present period is marked by decreases in traditional resources.

CANOPY AND TERRESTRIAL ARTHROPOD
 ABUNDANCE IN A BIG-LEAF MAPLE
 FOREST, QUINALULT RIVER, WA. Hugh
 Mortensen., Jeffrey Scott McKenzie.
 The Evergreen State College, Olympia,
 WA 98501

We conducted a 21 week study of canopy and terrestrial arthropods in an *Acer macrophyllum*-dominated river terrace community of Washington State. Berlese funnels extracted arthropods from samples taken in two canopy habitats (branch limb surface and branch junctions) of *Acer macrophyllum* Pursh trees, and the upper soil horizons beneath the trees. Arthropods were sorted into 24 taxa mostly at an ordinal level. The most abundant arthropods were collembola and mites. Abundances were similar in canopy and terrestrial locations. Collembola were significantly more abundant in the canopy, while mite and holometabolous larvae were significantly more abundant in terrestrial samples. Terrestrial samples averaged 1.7 times more taxa per sample than canopy samples. This study suggests that although canopy and terrestrial populations may be taxonomically distinct at the ordinal level, arthropod abundance in the canopy is similar to that found in the upper soil horizons.

CONSERVATION PLANNING IN THE GRASSLANDS OF HELLS CANYON: AN EXAMPLE FROM CRAIG MOUNTAIN, IDAHO. Robert K. Moselev and Michael Mancuso, Conservation Data Center, Idaho Department of Fish and Game, Boise.

Grasslands cover ca. 42,000 ha in the Salmon River and Snake River canyons surrounding Craig Mountain, at the north end of Hells Canyon. Over 1200 m of relief, along with high topographic and substrate variability, results in high species and community diversity. *Agropyron spicatum* and *Festuca idahoensis* are the primary community dominants, with shrublands and forests on favorable sites. Early settlement by European man consisted of a series of livestock ranches that proved uneconomical to operate, due largely to extremely rugged terrain and isolation. Most were eventually conveyed into public or private conservation ownership. Currently, five public and private institutions manage a vast majority of the Craig Mountain grasslands. All have a similar overall goal for the area, that is, conservation of native habitats and species. These institutions operate under different mandates, however, and specific objectives differ somewhat between institutions. A high level of coordination and cooperation is currently taking place relative to biological inventories, management plan development, restoration, and long-term monitoring strategies to accomplish our common goal of effecting large-scale landscape conservation in an efficient manner.

A VEGETATION STUDY OF A THIN-SOILED, MODERATELY DISTURBED SITE IN THE SHRUB-STEPPE OF EASTERN WASHINGTON. Melinda M. Mueller, Seattle Academy of Arts & Sciences, Seattle.

A significant portion of the Northwest's shrub-steppe consists of stony or thin-soiled sites, and study of such sites is needed if the ecology and effects of human disturbance on the shrub-steppe are to be understood. A species list, plant frequency and cover data, and soil-depth and associated Sandberg's bluegrass (*Poa secunda*) heights were collected at a thin-soiled site near Odessa, Washington during 1991-92. Species lists and plant frequency data were gathered at two additional locations in order to estimate grazing disturbances around the main study site. Analysis showed the study site to compare well with pristine sites, in spite of surrounding disturbance. Evidence was found for a relationship between the occurrence of different plant communities on the site and the depth of the underlying soil. Also, a relationship was seen between average soil depth and average height of Sandburg's bluegrass.

APPLYING CURRENT TECHNOLOGY TO DESIGN FISH VIDEO MONITORING SYSTEMS. Robert P. Mueller, Thomas J. Carlson, and Robert L. Johnson, Battelle Pacific Northwest Laboratory, P.O. Box 999, Richland, WA, 99352.

Recent advancements in video technology have enhanced the capability to record and document passage of fish over barriers. We found that high quality video images, can be produced using commercially available video technology. System components currently being developed include high resolution cameras, time lapse recorders, specialized lighting, imaging software, and optical storage devices. The systems can be used to gather qualitative and quantitative data without directly handling fish. Past operating practices, such as the use of artificial lighting and intermittent window cleaning, have resulted in a diminished ability to identify fish to species, determine their origin, and estimate lengths. Window cleaning protocols and the design of equipment to effectively clean the viewing glass are now being implemented at Prosser Dam on the Yakima River. Quantitative data such as detection of marks, tags, species identification, and morphometric characteristics can be measured. Video cameras will also be used to provide accurate measurements of water clarity.

The Canopy Research Network: A pathway for Interdisciplinary Exchange of Scientific Information on Forest Canopies

Nalini Nadkarni ¹, Geoffrey Parker ², David Ford ³, Judy Cushing ¹, and Cara Stallman ¹

Forest canopy communities are important in maintaining the diversity, resiliency, and functioning of the ecosystems they inhabit. With the increasing interest in forest canopies that is resulting from new access techniques, ecologists require tools to manage and analyze their data. With the support of the National Science Foundation, we established an organization to bring together forest canopy researchers, quantitative scientists, and computer scientists to establish methods to collect, analyze, and interpret three-dimensional spatial data relating to forest canopies. Our activities include: 1) compiling research questions from canopy scientists via a survey; 2) examination of potential information models and software tools that are in use in allied fields; and 3) development of conceptual models for information and analyses necessary to answer research questions posed by forest canopy researchers. We are also building a communications network (electronic and conventional); organizing the published canopy literature; and serving as a repository for canopy information that is accessible to scientists, forest managers, and the general public.

¹ The Evergreen State College, Olympia, WA 98505, Smithsonian Environmental Research Center, Edgewater, MD 21038, Center for Quantitative Studies, University of Washington, Seattle, WA 98195

LICHEN ABUNDANCE AND DIVERSITY ALONG A CHRONOSEQUENCE FROM YOUNG MANAGED STANDS TO ANCIENT FOREST, WESTERN CASCADES, OREGON. Peter Neitlich, Oregon State University.

The ecological importance of lichens in late-successional forests is increasingly appreciated, but little is known about the effects of forest management on lichen populations. This study used litterfall and biodiversity survey plots to compare the species richness and biomass of epiphytic macrolichens in 3 old growth (510 y), 3 mature (140 y), 3 rotation-age (70 y) and 3 young (40 y) stands within the *Tsuga heterophylla* zone. Lichen biomass in old growth stands (4.7 t/ha) was approximately 30 times that of young stands (0.2 t/ha), 6 times that of rotation-age stands (0.7 t/ha) and 3 times that of mature stands (1.5 t/ha; $0.001 < p < 0.04$). Old growth forests contained two-thirds of the pooled lichen biomass of all four age classes. Forests 140 y old or older contained 90% of the pooled lichen biomass of all four age classes. Mature and old growth forests had 40% more lichen species than young and rotation-age forests ($p < 0.03$). Results suggest that conversion of old growth to young managed stands has reduced cyanolichen N-fixation in these stands to <3% of former levels, has decreased lichen-associated canopy arthropod populations to 25% of former levels, and has diminished the availability of commonly used forage and nesting materials for birds, small mammals, and ungulates.

RESPONSE OF SMALL MAMMAL POPULATIONS TO BIOSOLIDS APPLICATION ON DOUGLAS-FIR FORESTS. Sally Nickelson, Point No Point Treaty Council, Kingston.

Over the past 15 years, several studies have examined the use of biosolids as a forest fertilizer, but only a few have concentrated on wildlife responses to the application. I studied small mammal and habitat changes four years after biosolids amendment to Douglas-fir forests in the Pacific lowlands. Sites receiving two different doses of biosolids were utilized and compared with matching controls. Trapping took place in spring and fall of 1992. Herbaceous vegetation and deciduous shrubs had significantly greater mean percent cover on all treatment sites as compared to controls. During fall, *Microtus oregoni*, *Neotrichus gibbsii*, *Peromyscus maniculatus*, *Sorex monticolus*, and *Sorex trowbridgii* all had significantly greater numbers than expected on high dose treatment sites. On the low dose sites, *Microtus oregoni* and *Peromyscus maniculatus* had significantly higher catch than expected. Catch of small mammals during spring trapping was relatively low, and only one species, *Sorex monticolus*, had significantly greater numbers present on the high dose treatment sites. No small mammal species had significantly lower numbers on treatment sites. Community composition (percent of capture contributed by each species) on all treatment sites had a much more even distribution of species than did controls.

FACTORS AFFECTING FRUIT SET BY *PENSTEMON HARRINGTONII*. Romaine L. Nielson, Utah State Univ., Logan, and V. J. Tepedino, USDA, ARS, Utah State Univ., Logan.

P. harringtonii is a rare perennial of three river valleys of Colorado. Because restoration of some threatened populations in developing areas may be necessary, we examined the breeding system, and compared the reproductive success of plants growing in different microhabitats, and at different densities. Flowers were self-compatible but did not set fruit unless visited by insects, especially native bees. Plants within sagebrush canopies did not differ from those in the open in rate of fruit set except that those in sagebrush set most fruits at the top of the inflorescence and those in the open set most fruits in the middle. Plants in clumps of three set fewer fruits/inflorescence than did single plants in the open. The results suggest that fruit production is resource, rather than pollinator, limited.

CHARACTERISTICS OF SPRING FORAGING ECOLOGY AMONG BLACK BEARS (*Ursus americanus*) IN THE CENTRAL COAST RANGES OF OREGON. William O. Noble and E. Charles Meslow, Oregon State University, Corvallis.

Spring is generally a negative foraging period for black bears. During this period, some bears peel the bark off trees and ingest the cambium. We investigated cambium-feeding by bears, a monogastric species, and characteristics of the resulting tree damage. We compared food habits, based on scat analysis, between bears in adjacent study areas. Small volumes of a variety of forbs and cambium occurred with greater frequencies in scats from bears in an area with high damage levels (north area) than in scats from bears in an area with low levels of damage (south area). Scats from the south area had greater frequencies of berry-producing shrubs than did scats from the north area. Damage levels and characteristics were quantified by surveying 40 randomly selected forest stands in each area. Results indicate bears selected stands and individual trees that maximized cambium production. Tree plantations resemble continuous patchy habitat. Foraging costs in these habitats, combined with seasonal attributes of tree physiology and bear morphology, suggest cambium-feeding may be an energy efficient forage for some bears during spring despite their inability to digest cellulose.

A COMPARISON OF CANOPY STRUCTURE IN THREE FOREST STAND TYPES. Malcolm P. North, College of Forest Resources, University of Washington, Seattle, WA.

Tree canopies are an important but poorly understood element of forest ecosystems. Few quantitative measures of canopy structure have been developed because: 1) measurements are difficult to make; 2) there is no agreement on an appropriate scale or measurement unit; 3) a comparable index of complex three dimensional space has not been developed. This study is an exploratory comparison of canopy structure using ground-based, stand-level measurements taken in three forest types: managed mature (clearcut and burned in the 1920's), natural mature (wind disturbed in 1921) and old growth. Two measures were compared between stands: the percent of available canopy space occupied by tree crowns, and the diversity of vertical foliage layering. Old growth compared to managed mature showed a higher percent of available canopy space occupied by foliage ($p < 0.05$) and much greater diversity of foliage layering ($P < 0.001$). Natural mature stands are closer to old-growth than managed-mature stands in their canopy structure. This comparison suggests: 1) canopy structure is strongly influenced by stand origin as well as stand age and 2) ground-based measures can discern differences in canopy structure.

A COMPARISON OF LIFE HISTORY AND CENSUS STUDIES IN DETERMINING HABITAT USE BY THREE NEOTROPICAL MIGRANTS. Scott F. Pearson and David A. Manuwal, University of Washington, Seattle.

Point count censuses of singing male passerines provide landscape level information on density and patterns of distribution. Life history studies of these birds can identify specific habitat features associated with reproduction. We compared density and distribution patterns from census studies, with habitat features associated with nest sites and territories for the Pacific-slope Flycatcher, Hermit Warbler, and Townsend's Warbler in the southern Cascades of Washington. Data from point count censuses indicated an increasing density of territorial male Pacific-slope Flycatchers with stand age. A life history study of the flycatcher revealed the importance of red alder as a nesting substrate and deciduous trees for nesting sites. For Hermit and Townsend's Warblers, point count data indicated a higher density of the two species in younger forests and in dry old-growth forests. Habitat analyses centered on territorial male warblers indicated that Hermit Warblers use sites with relatively high structural diversity. Townsend's Warblers used sites with high foliage volumes of conifer trees. Life history studies provide valuable insights into the habitat features associated with nest sites and territories that are not necessarily revealed by census studies.

GREEN TREE RETENTION AND CANOPY LICHEN COMMUNITIES. JeriLynn E. Peck, Bruce McCune, Oregon State University, Corvallis.

Understanding the impact of green tree retention on canopy lichen communities is essential for evaluating the effectiveness of "new forestry" practices aimed at increasing biodiversity. To evaluate this impact, we sampled canopy lichen biomass in paired natural stands; one stand approximated green tree retention cuts with old-growth over rotation age regeneration, the other lacked old-growth. Lichen litterfall was collected in fourteen sites within the Willamette National Forest in the Oregon Cascade Range, all within the *Tsuga heterophylla* Zone. Three functional groups of canopy lichens were distinguished: cyanolichens that include cyanobacteria (mostly *Lobaria oregana*), alectoroid lichens that are pendulous (*Usnea*, *Alectoria*, *Bryoria*), and other lichens that include all other macro-lichens (*Hypogymnia*, *Platismatia*, etc.). Cyanolichen biomass was lower in nonretention plots in areas with less surrounding old-growth, suggesting that dispersal from propagule sources (retention trees) may be an important factor affecting cyanolichen distribution. Distance to water, the number of live stems per plot, and the number of *Tsuga* retention trees also affect cyanolichen biomass. The squareroot biomass of other lichens and alectoroid lichens varied as a function of their elevation and vertical distance from water. Other lichen biomass was lower with larger amounts of surrounding old growth. The effectiveness of green tree retention for maintaining canopy lichen biodiversity may be dependent on the number of retained trees within a several hectare area surrounding a given point.

TREE CLIMBING AS A TECHNIQUE FOR LOCATING MARBLED MURRELET NESTS. Robert W. Peck, S. Kim Nelson, and Toni L. De Santo, Oregon Cooperative Wildlife Research Unit, Oregon State University, Corvallis, OR 97331.

Marbled Murrelets (*Brachyramphus marmoratus*) are unique among seabirds in their nesting habits, using arboreal nests within mature and old-growth coniferous forests, and choosing nest sites on large limbs and deformations within the canopy. Of 64 known nests, most were found by observing birds flying into trees at dawn or searching for eggshells on the forest floor. This paper presents results from our 1993 study which used a new nest search technique, intensive tree climbing, to locate nests. During the tree climbing study, 28 of 40 trees with potential nest platforms were climbed within a 70 m-radius plot using ropes and ascenders. Six nests were found (5 measured) within the upper portions of 5 trees. Nest platforms averaged 49.4 m above the ground (SE=4.6), 57.2 cm from the trunk (SE=22.8), and 35.6 cm in width (SE=6.8). An accumulation of tree-borne debris in and around the nests indicated that the nests were not active during 1993. Characteristics of these nests were similar to the 16 nests previously found in Oregon. Additional climbing plots will allow quantitative identification of nest site characteristics and determination of nest density within the stand.

FIRE MANAGEMENT AND REHABILITATION STRATEGIES TO MAINTAIN SHRUB STEPPE COMMUNITIES IN SOUTHERN IDAHO. Mike Pellant, Bureau of Land Management, Boise, Idaho.

Alien plants and wildfires have dramatically altered ecosystem function in southern Idaho. The use of fire resistant vegetation i.e. greenstrips and diverse seed mixtures in rehabilitation projects can reduce or mitigate wildfire impacts. Greenstrips are living "fire barriers" planted at strategic locations on the landscape to reduce wildfire size and frequency. Since 1985, 450 miles of 30- to 400-ft-wide greenstrips have been planted in Idaho. A BLM sponsored research project has provided new plant materials and seeding strategies for use on fire-prone landscapes. Wildfire rehabilitation practices can partially restore structure and diversity on burned rangelands. However, proper seeding equipment and availability of native species have limited the ability of land managers to reestablish plant diversity after wildfires. Procedures to successfully establish big sagebrush (*Artemisia tridentata*) and winterfat (*Ceratoides lanata*) have been developed. Integrating understory plants that are fire resistant with native shrubs on rehabilitation projects will promote long term stability of plant communities in the fire-prone environment of southern Idaho.

PLANTING OF RIPARIAN VEGETATION ALONG THE SNAKE RIVER IN WASHINGTON STATE. Ronald C. Phillips, Battelle, Richland. Lonnie Mettler, Army Corps of Engineers, Walla Walla.

An experimental drawdown of the Snake River was conducted in two reservoirs during March 1992. Five species were planted at four sites at four elevations each in March 1992. Monitoring occurred monthly through July 1992, and once in May 1993. *Carex obnupta* demonstrated the best survival, minimal areal expansion, but the greatest resistance to grazing by Canada geese (very numerous at Alpowa and Chief Timothy sites). While *Scirpus validus*, *Carex aperta*, and *Eleocharis palustris* were decimated at these two sites, survival and areal expansion were high at Deadman Creek. *Deschampsia caespitosa* survived well at most elevations at Alpowa and Chief Timothy. *Scirpus*, *Deschampsia*, and *Eleocharis* demonstrated abundant flowering and fruit production. *Deschampsia* was intermediate in grazing preference and survival among the five species.

RECENT CLIMATIC TRENDS ON THE COLUMBIA PLATEAU AND EXAMPLES OF WETLAND RESPONSE. Robert R. Quinn, Eastern Washington University, Cheney.

The recent drought of 1985-1992 has been long lasting and severe on the Columbia plateau. Palmer drought indexes of -1.50 to -3.0 (moderate to severe) have been persistent from 1985-1992 in all climatic divisions. Permanent and seasonal wetlands have been severely impacted. Over 80% of the permanent wetlands were dry in Spokane county by September of 1992. Wetland vegetation reflected rapid succession of invasive Reed canary grass into locations normally occupied by aquatic bed vegetation. The wetter winter of 1993-94 and record wet July has brought regionally erratic recovery to the scablands with substantial filling of wetlands in Spokane County and only modest recovery in the Columbia Basin. Comparable droughts occurred in the 1920's and 1930's but were of shorter duration and more modest magnitude.

A NOOSE TRAP FOR CAPTURING PILEATED WOODPECKERS. Catherine M. Raley and Keith B. Aubry, U.S. Forest Service, Pacific Northwest Research Station, Olympia, Washington.

Several techniques have been developed for capturing pileated woodpeckers (*Dryocopus pileatus*), but these methods use spring-loaded board or net traps and have limited applicability. We captured 16 pileated woodpeckers on the Olympic Peninsula, Washington, using noose traps. Noose traps have several advantages over other methods: they can be applied any time of year, they do not require birds to enter cavities, and they are easy to construct.

REPRODUCTIVE ECOLOGY AND POPULATION GENETICS OF BLACK COTTONWOOD IN RIPARIAN ECOSYSTEMS. John Reed and Steve McKay, University of Washington, Seattle.

Black cottonwood is experiencing widespread habitat degradation that may lead to changes in reproductive ecology and alter genetic patterns and processes. This presentation describes two studies, one investigating the impact of river regulation on the reproductive ecology of black cottonwood, the second investigating the patterns and underlying causes of its genetic variation in the Yakima river valley. The first study examines the importance of non-clonal vs clonal regeneration in dammed and undammed reaches of the Cowlitz and Nisqually rivers. In the second study molecular data show that the upper and lower portions of the Yakima are genetically differentiated, possibly due to climatic differences. Also, the upper Yakima is more genetically diverse than the lower, possibly reflecting different reproductive modes. Completion of these two studies should reveal how river regulation and climate interact in affecting black cottonwood reproductive ecology and population genetics.

NEST SITE RELATIONSHIPS AMONG CAVITY-NESTING BIRDS IN ASPEN WOODLANDS OF SOUTHEASTERN OREGON. Adam C. Rich and David S. Dobkin, High Desert Ecological Research Institute, Bend, OR.

Cavity-nesting bird species constitute nearly 50% of all breeding individuals in riparian and snowpocket aspen woodlands in southeastern Oregon. Red-naped Sapsuckers and Northern Flickers are the primary cavity excavators in these habitats and provide significantly different sizes of nest holes for a suite of secondary cavity-nesting birds. We used univariate and multivariate analyses to compare physical and biological attributes of nest sites among cavity-nesting birds and found varying degrees of overlap among species in nest site characteristics. House Wrens exhibited the greatest variability in nest sites and thus appeared to be the most plastic in their nest cavity requirements. Tree Swallows appeared to be most dependent on sapsuckers for nest cavities. Mountain Bluebirds and European Starlings primarily utilized flicker-excavated cavities and may compete with each other for nest sites. We suggest starling removal and nest box studies to test hypotheses regarding nest-site competition.

SHRUBSTEPPE PLANTS OF THE HANFORD SITE: DISTRIBUTION AND ABUNDANCE. W. H. Rickard and Janelle Downs, Pacific Northwest Laboratory, Richland, Washington.

The distribution and abundance of shrubsteppe plants, especially shrubs and grasses on the U.S. Department of Energy's Hanford Site in southcentral Washington, varies across the Columbia River plain and in the adjacent Rattlesnake Hills. This area is unique from other shrubsteppe areas in Washington because it has been free from livestock grazing for 50 years. Canopy cover and density measurements were used to describe stands. Species composition is related to past land use practices, particularly farming, recent wildfires, perched water tables, dry lake beds, soil texture and stoniness, and microclimate as influenced by elevation. This work was performed under contract DE-AC06-76RLO 1830.

VARIATION IN REPRODUCTIVE STRUCTURES FOR RARE AND COMMON SPECIES OF *ERIGERON* L. (ASTERACEAE): EXPLORING PATTERNS OF ENDEMISM. K.A. Robson^{1,2}, C.C. Hanson^{1,2}, & W.W. Barker¹, ¹Rare Plant Consortium, Central Washington University, Ellensburg; ²USDA PNW Research Station, Wenatchee, WA.

Erigeron, a large genus including both rare and widespread species, is a good subject for comparative studies in a phylogenetic framework. Floral structures were measured for two rare (*Erigeron basalticus* and *E. piperianus*) and three widespread (*E. linearis*, *E. pumilus* and *E. poliospermus*) fleabane daisies, all desert natives of eastern Washington. Each species studied is represented by ten flowering heads from ten individuals in single populations. Lengths of disk corollas, pappus and achenes (cypselsas) are compared among species, as separate variables (box plots) and in combination (factor analysis) to better understand how a restricted genetic base is expressed structurally. The rare species show less variation in some reproductive variables, but organization among variables is not strong. These patterns may be manifested as an inability to expand or compete beyond narrow ranges.

EXOTIC PLANTS OF THE SHRUB STEPPE. Ben E. Roché, Jr., Washington State University, Pullman.

The shrub steppe has been and remains severely impacted by preadapted Eurasian exotics. The bell-wether was cheatgrass (*Bromus tectorum*). It invaded the west in the 1890s as a weed in grain fields. Twenty-five years later it was occupying the niche created by mismanagement and hence weakening of the native bunchgrasses. For a time, forty years or so, varying with location, cheatgrass dominated the understory of most poor or fair conditioned shrub steppe ranges. Since the 1950s, *Centaurea* species present since the turn of the century have invaded and, in many instances of continued mismanagement, become the codominant if not dominant understory species. Diffuse knapweed (*C. diffusa*) and squarrose knapweed (*C. virgata* spp. *squarrosa*) have demonstrated the greater affinity for the sagebrush/bunchgrass habitat type. Diffuse knapweed, first collected in Klickitat County, Washington in 1907, is rampant in the Pacific Northwest and extending into the southern reaches of the vegetative zone. Squarrose knapweed, first recorded in Larson County, California in 1950 and Juab County, Utah in 1954, is making its way north. Range ecologists no longer accept that range plant communities change along a well-defined, predictable and reversible successional gradient. It is becoming obvious that within a managerial time frame poor and fair condition ranges (early and midseral) aren't capable of autogenic improvement. They appear to be an arrested succession.

CANOPY - ATMOSPHERE INTERACTIONS. Catherine L. Rose, PNW Research Station, Bend, OR.

Scientific interest in canopy-atmosphere interactions has accelerated during the past decade. Earlier emphasis on whole-tree physiology has expanded to include stand, landscape, ecosystem, and global-level processes. An improved understanding of canopy-atmosphere interactions has particular relevance to many urgent issues in global change (pollution, climate) and forest health. This paper presents an overview of past and present research in canopy-atmosphere interactions in the Northwest and highlights new opportunities for the future.

ECOPHYSIOLOGICAL PROCESSES IN CROWNS AND CANOPIES OF PONDEROSA PINE FORESTS IN THE CENTRAL OREGON CASCADES. Catherine L. Rose, PNW Research Station, Bend, OR.

Traditional silvicultural studies in eastside forests have focused on describing the effects of forest management practices on tree growth. New research approaches are needed to provide a more integrated and mechanistic understanding of forest health and productivity. Canopy processes are a critical and little-known component of forest response. Planned and on-going research with Ponderosa pine (*Pinus ponderosa*) in central Oregon combines silvicultural assessment of forest growth with ecophysiological studies of tree canopies. A variety of new studies, approaches, and future opportunities in canopy research are described.

CANOPY LICHENS AND HOW TO MEASURE OTHER RELEVANT ENVIRONMENTAL SITE CONDITIONS IN CENTRAL IDAHO. Roger Rosentreter, Bureau of Land Management, Boise, Idaho.

The composition and biomass of the canopy lichens should be determined relative to other environmental site conditions. What other environmental conditions are relevant to the occurrence of lichens and how to measure these conditions needs further study. Other environmental conditions measured in Central Idaho were: habitat type, cover type, tree composition, canopy density, canopy layers, basal area, tree size classes, coarse woody debris by decay class, distance to nearest forest opening, and distance to nearest tree greater than average diameter size class (legacy tree). Lichen cover and biomass should be correlated with these other environmental conditions to assist with active forest management prescriptions and mitigation.

LICHENS OF THE SHRUB STEPPE Roger Rosentreter Bureau of Land Management, Boise, Idaho.

Lichens are a major component in the shrub steppe ecosystem, as they are well adapted to the region's arid climate. The composition, structure, and function of lichens in the shrub steppe will be related to the overall biodiversity of this ecosystem. Some of the common species will be highlighted and characterized. Lichens grow epiphytically on the shrubs and frequently cover the soil surface. Many of the soil-occurring species penetrate the soil surface and form a shallow rooting zone. The major functions of lichens are in the binding of soil, increased soil moisture infiltration and retention, and nitrogen fixation. These lichens act as an organic mulch by shading, cooling, and decreasing evaporation of soil moisture. Soil moisture and its seasonality is a critical factor in the ecology of the shrub steppe.

SOILS OF THE NORTHERN COLUMBIA PLATEAU. Gerald B. Rouse, USDA Soil Conservation Service. Spokane, WA.

Major soil associations and complexes in the Columbia Basin, loess uplands, and scablands are identified, located, and discussed by reference to soil properties and morphological features. The major soil associations are then related to the historic climax plant community and potential natural community with implications for soil stability, watershed function, and ecosystem management. Alternative classification systems, such as Major Land Resource Areas and Ecoregions, are discussed and related to soils and plant criteria.

THE FOREST SERVICE'S WESTERN FOREST CARNIVORE CONSERVATION ASSESSMENT. Leonard F. Ruggiero, USFS Rocky Mountain Research Station; Keith B. Aubry, USFS Pacific Northwest Research Station; Steven W. Buskirk, University of Wyoming; L. Jack Lyon, USFS Intermountain Research Station; William J. Zielinski, USFS Pacific Southwest Research Station.

A cooperative effort by Forest Service Research and the National Forest System is underway to summarize what is known about the biology, ecology, and conservation status of the American marten, fisher, lynx, and wolverine in the mountains of the western U.S. (excluding Alaska). This book will also discuss the management implications of existing information, and identify additional information needed for the development of scientifically sound conservation strategies. Boreal forest habitats in the western mountains, where all four species occur, are more fragmented and isolated in distribution than those in northern regions. For this and other reasons, the forest carnivore populations in the western U. S. are of special management concern.

PRILIMINARY OBSERVATIONS OF SEASONAL PATTERNS OF GROWTH IN *BOTRYCHIUM*. Steven K. Rust and Elroy Burnett, USDA Forest Service, Lake Wenatchee Ranger District, WA.

Phenological data on rare species of *Botrychium* were collected to improve ecological understanding and inventory reliability. Plant data were collected at populations over an elevation gradient within the Little Wenatchee River drainage, WA. Census, growth and environmental data were collected, May - July, 1993, at three sub-samples within each of seven population sites. Species observed were: *B. lanceolatum* (BOLA), *B. manganense* (BOMI), *B. montanum* (BOMO), *B. paradoxum* (BOPA), and *B. pinnatum* (BOPI). Plants were detectable as snow melted at both low and high elevations. In many plants, species was not determinable through June. Three patterns of plant growth were observed: early initiation of steady growth (BOMI & BOPA); early initiation of rapid growth (BOLA & BOPI); and continuous initiation of steady growth (BOMO). Growth patterns appear to be related to environmental factors of preferred habitat. Early, rapid growth may be advantageous in lush meadow (BOLA & BOPI) where, compared to coniferous forest (BOMI & BOPA), herb cover is high. Initiation of growth in BOMO may occur periodically throughout the growing season in response to favorable moisture availability.

MANAGEMENT OF OREGON WHITE OAK (*QUERCUS GARRYANA*) WOODLANDS FOR BIODIVERSITY. Loreen Ryan and Andrew Carey, USDA FS, PNW Research Station, Olympia, WA 98512

At least 25 species of wildlife, including seven sensitive and threatened species, depend on Oregon white oak woodlands. Oak woodlands have been reduced in number and size and will require management to maintain their biodiversity and quality as habitat. In the past, oak woodlands were maintained by repeated burning that reduced encroachment of Douglas-fir (*Pseudotsuga menziesii*) allowing oaks to achieve a large open form. Because of fire suppression, alternative management is necessary to prevent oak woodlands from converting to Douglas-fir forests. Management goals include: large areas of open-form oak stands with adjacent intergrading conifers, prairies, and wetlands; reduced fragmentation; open to patchy understory devoid of invasive species such as scotch broom (*Cytisus scoparius*); and reduced human disturbance to prevent root damage. Management applications include removing overtopping Douglas-fir trees (except old-growth), thinning dense understory oak and Douglas-fir to release remaining oaks; maintaining or developing habitat corridors to link oak patches; prescribed burning to reduce invasive shrub competition; and promoting oak woodland conservation on public and private lands through information, education, and legislation.

A LIMNOLOGICAL STUDY OF A SOUTHERN OREGON CASCADE LAKE: LAKE OF THE WOODS. John T. Salinas, The Cascade Research Group, Murphy, OR.

Lake of the Woods is located on the east slope of the Cascade Range, 25 miles north-northwest of Klamath Falls. The area is estimated to support over 130,000 people-days per year.

Lake of the Woods is a mesotrophic lake with unusual biological and physical conditions. A study of the lake was begun in 1992 to document existing lake conditions. Research included using *in situ* instrumentation and grab samples. Anoxic conditions found in the hypolimnion may produce an internal source of nutrients for the lake. Phosphorus concentrations have been very low suggesting that any change in this single nutrient would drastically change the lake. Unique assemblages of phytoplankton and zooplankton have raised questions concerning how lake history and ground water movement have lead to current lake conditions.

A trophic state index of 38 has been calculated using chlorophyll concentration, Secchi disk clarity, primary productivity, and algae biomass.

DISTRIBUTION PATTERNS OF RARE PLANTS IN WASHINGTON. Debra Salstrom, Washington Natural Heritage Program.

Plant species classified as rare in Washington have one of the following patterns of distribution: endemic, disjunct, peripheral or scattered. This discussion will focus on the distribution patterns of these groups in Washington. These patterns will be correlated to areas of the species origin and past climatic patterns. In addition, the influence of length of time in isolation, life form and breeding system on the type of rarity and amount of genetic variation within and between populations will be discussed.

IN SEARCH OF WASHINGTON STONEFLIES. Cordia J. Sammeth, Gerald F. Kraft Western Washington University.

The presence, abundance, and species composition of Plecoptera in a stream are useful parameters for assessing habitat quality. Protocols that produce the highest level of credibility from bioassessment require macroinvertebrate identification to the species level. The nymphs of stonefly families are easily recognized, and genera readily keyed, but the nymphs of many species can not be identified because they are inadequately described or quite unknown. Biological information is generally available on common genera, but many of our species are unknown biologically. A recent list (1992) of stoneflies known to occur in Washington cites 100 species. A search of literature, an examination of specimens in collections at Central and Western Washington Universities, and recent statewide collecting suggest the presence of more than 125 species. The outcomes of efforts to revise the list of Washington species, to describe nymphs, and study life histories will complement current knowledge of stonefly biology, and provide sharper tools for rapid bioassessment of streams.

HISTORY OF LAND MANAGEMENT ON SHRUB STEPPE LANDSCAPES ADMINISTERED BY THE BUREAU OF LAND MANAGEMENT IN THE PACIFIC NORTHWEST. Alan R. Sands, Bureau of Land Management, Boise, Idaho.

The management activities of the agency are reviewed for the 40-year period 1950 - 1990. These include an overview, by state (WA, OR, and ID), of land disposal/acquisition, fire, brush control, seedlings, water developments, and livestock use. These activities coupled with other human-induced changes have had a significant impact on shrub steppe landscapes as indicated by current ecological conditions, extent of exotic annual invasion, and the risk of further degradation of these landscapes. Recent efforts to improve shrub steppe ecological conditions and reduce fragmentation of the landscape are discussed.

MOVEMENT AND HABITAT USE OF SAGE GROUSE IN A FRAGMENTED LANDSCAPE.

Michael A. Schroeder, Washington Department of Wildlife, P.O. Box 1077, Bridgeport, WA 98813.

Sage grouse (*Centrocercus urophasianus*) are endemic to the shrub steppe habitats of western North America. Large-scale degradation and removal of habitat as part of various agricultural practices has resulted in the dramatic reduction of sage grouse populations in numerous portions of their range, particularly in Washington. Remaining populations are restricted to relatively small patches of habitat in Kittitas, Yakima, and Douglas counties. Research was initiated in 1992 to examine movement and habitat use of sage grouse captured on display sites (leks) in Douglas County, Washington. Although 67% of 9 sage grouse leks were in wheat, 81% of 47 nests were in relatively thick sagebrush/grass cover, often in remnant areas of shrub steppe habitat bordered by wheat. The average distance between nests and the nearest lek was about 5 km. In other studies conducted in relatively continuous habitats, most female sage grouse apparently nested within 3 km of the nearest lek. Although nest locations frequently were dominated by either threetip sagebrush (*Artemisia tripartita*) or big sagebrush (*A. tridentata*), virtually all winter locations were in large areas dominated by big sagebrush. Distances between breeding and winter locations averaged 17 km for females and 11 km for males.

CHALLENGES OF MANAGING SMALL NATURAL AREAS WITHIN THE SAGEBRUSH ECOSYSTEM. Reid Schuller, Natural Area Preserve Program, Washington Department of Natural Resources, Olympia.

Historical and contemporary land management practices have led to extensive alteration of the shrub steppe ecosystem of central and eastern Washington. Remaining natural or semi-natural areas do persist. However, they are typically small in size, and are effectively isolated from one another. Scientists and managers of natural areas are challenged to maintain or restore ecosystem integrity in the face of these less-than-ideal landscape settings, while recognizing the increasing importance of legal, economic, political, and community issues.

TRADITIONAL AND NON TRADITIONAL ARBORICULTURAL TECHNIQUES USED IN CONJUNCTION WITH PLATFORMS AND WALKWAYS TO AID THE RESEARCHER IN CANOPY ACCESS AND SITE EVALUATION. Jon Shaffer, Portland Oregon, . Kevin Hillery, Portland Oregon, . Donna Attewell, Portland Oregon.

Out of necessity, arborists have developed techniques to access all areas of the forest canopy. Standard arboricultural practices such as site evaluation and preservation, hazard identification, assessment of the long and short term stability of research areas are directly applicable to canopy research. From this base of knowledge new techniques have been created to minimize impact to the forest. Incorporating these methods and practices allows the researcher to maximize use of resources, collect more data and produce more concrete results in less time, thus furthering the possibility for continued research. Adoption of these methods and practices enhances safety for the climber and the tree.

CANOPY DWELLING BIRDS Fred A. Sharp
Simon Fraser University, Burnaby BC, V5A 1S6
Canada

Flight and arboreal living have produced many opportunities, as well as limitations, for canopy dwelling birds. These adaptations include high basal metabolism, the use of contrasting seasonal habitats, high mobility, diurnal activity patterns, and specialized requirements for nesting and nocturnal roosting. Several methods can be used to examine avian use of canopy habitats, including the influence of environmental factors at different habitat scales. Important macroscale factors affecting bird richness and abundance in canopies include precipitation, elevation, latitudinal effects, and forest isolation. Critical mesoscale or stand level attributes include tree composition, structural attributes, foliage height diversity, canopy gaps, slope, aspect, stand history, seasonality, and understory development and primary productivity of seeds, fruits and arthropods. The use of microsites is governed primarily by tree architecture, rot characteristics, foliage type, bark texture, and epiphyte loading. The highest avian richness and/or abundance is often attained in the canopies of older forest types or riparian communities. In contrast, the canopies of coastal red cedar forests are characterized by impoverished avian assemblages. Factors influencing habitat selection of canopies will be discussed, as well as the influence of ontogenetic variation, sexual dimorphism, intra and interspecific competition and historical association with specific habitat types.

FOREST CANOPY ECOSYSTEM FUNCTIONS. David C. Shaw, University of Washington, Seattle.

Northwest forest canopy ecosystems can be classified into three functional types: urban, riparian/wetland and upland/terrestrial. Urban forest canopies act to abate noise, ameliorate urban "heat sink" temperature increases, conserve energy by providing shade for buildings, and remove dust, pollutants, and carbon dioxide from the air, thus making cities more livable. Riparian/wetland forest canopies affect temperature and primary production of aquatic habitat by shading, influence productivity by controlling allochthonous inputs including coarse woody debris, and provide unique habitat for wildlife and other biota. Upland/terrestrial forest canopies drive the carbon cycle, fuel the below-ground biological decomposition systems, influence forest nutrient cycling by fixing nitrogen and by capturing, cycling and transforming nutrients within the canopy, interact with the atmosphere to modify and influence local and regional climate, affect watershed hydrologic regimes, and contribute to biodiversity. In general, canopy composition, age, and structure have a direct influence on these ecosystem functions. Traditionally, research within each of these three forest canopy systems has been carried out under a separate discipline, i.e. urban canopies by arborists, riparian canopies by stream ecologists, and terrestrial canopies by forest ecologists. However, to gain a complete understanding of how forest canopies influence regional ecosystem function both physically and biologically, we must integrate our collective knowledge.

CANOPY MACROLICHENS IN SECOND-GROWTH WESTERN HEMLOCK, SAPPHO, WASHINGTON. David C. Shaw, Kobe Harkins and David Woodruff, University of Washington, Seattle.

Canopy macrolichens were sampled using the litter "pick-up" method at the Sappho, Washington, Long Term Site Productivity, Intergrated Research Site, Fall 1993, in 60 year old western hemlock (*Tsuga heterophylla*). Two hundred, 2 meter radius, circular plots were laid out at established grid-points over 40 long term productivity treatment plots (5/plot). The purpose of the study was to determine relative abundance of lichen functional groups (alectorioid lichens, cyanolichens, and "other" lichens) as a baseline prior to silvicultural manipulations which will maintain treatment blocks in various stages of succession (early, mid, and late, plus control). Seventeen percent of the plots had no lichens. "Other" lichens occurred on 70.5% of the plots, dominated by *Hypogymnia* (67% freq.), *Platismatia* (26% freq.) and *Sphaerophorus* (10.5% freq.). Alectorioid lichens occurred on 13% of the plots, both *Usnea* and *Alectoria* present, but in small quantities. Cyanolichens occurred on 40% of the plots, dominated by *Nephroma* (31.5% freq.) and *Sticta* (12% freq.). The high frequency of cyanolichens was unexpected.

DIEL AND VERTICAL DISTRIBUTION VARIATION OF EPIPHYTE GRAZERS IN A TEMPERATE EELGRASS (*ZOSTERA MARINA*) SYSTEM. Travis C. Shaw, Department of Biology, Western Washington University, Bellingham, Washington.

The vertical distribution and abundance of four epiphyte grazer taxa was monitored over the diel cycle for 3 months in Padilla Bay, Washington. Samples were collected weekly from the basal, intermediate and apical portions of *Zostera marina* turions during the day and at night. Each of the four grazer taxa showed temporal variation in abundance. The vertical distribution of *Idotea ressecata*, *Phyllaplasia taylori* and caprellid amphipods shifted during the diel cycle. All three grazers moved toward the apical end of the eelgrass shoots at night during periods of maximum abundance. Temporal and diel changes in grazer abundance allowed wider utilization of the epiphyte resource.

BODY TEMPERATURE VARIATION OF ROCK SQUIRRELS DURING HIBERNATION IN SOUTHEASTERN IDAHO. Stephen R. Shoemaker and Berry L. Keller, Idaho State University, Pocatello, Idaho.

Rock squirrels (*Spermophilus variegatus*) are at the extreme northern end of their distribution in the Oneida Narrows Canyon in Southeastern Idaho. They have been characterized as "relatively poor" hibernators by previous researchers based on high levels of normothermic activity when maintained at ambient temperatures of 3°C in the laboratory. I monitored body temperature (T_b) continuously over the course of a hibernation season with an implanted temperature sensitive radiotransmitter in a squirrel in its natural burrow. Transmitter pulse intervals were recorded every half hour with a timer-controlled audio recording system and analyzed in the laboratory to yield body temperatures. Environmental temperatures were monitored with a thermocouple array and recorded onto a datalogger. The pattern of T_b s exhibited showed a pattern similar to that of other ground squirrels known to be efficient hibernators, characterized by long periods of decreased T_b interspersed with periodic arousals. Minimum body temperature attained decreased and hibernation bout length increased throughout the season until mid February when T_b no longer dropped below normothermic levels. T_b never fell below 9°C even though deep ground temperature was at times below 0°C. There does not appear to be a direct relationship between the timing and length of hibernation and environmental temperature.

GROWTH RATES OF TWO OLD-GROWTH-ASSOCIATED CYANOLICHENS IN THE CANOPY OF A 700 YEAR OLD DOUGLAS-FIR FOREST IN WESTERN OREGON.

Stephen C. Sillett, Oregon State Univ., Corvallis.

Live thalli of *Lobaria oregana* and *Pseudocyphellaria rainierensis* were collected from the crowns of 2 large Douglas-fir trees, one growing in the interior of the forest and one growing on the edge of a 20 year old clearcut. Thalli were cleaned of debris and cut into pieces (cuttings) 5-10 cm in length, 2-5 cm in width, and including at least 2 growing lobe tips. Individual cuttings were attached to small loops of monofilament with silicone. A total of 400 cuttings were prepared, 200 of each species, half from thalli collected in the interior and half from thalli collected on the edge. Cuttings were transplanted into the crowns of 4 large Douglas-fir trees, 2 growing in the interior and 2 growing on the edge. Transplants remained in the canopy for one year. Half of the transplants in each tree were derived from thalli collected in the interior and half were derived from thalli collected on the edge. 2-way ANOVA with trees as the units of replication revealed 2 significant treatment effects. *L. oregana* transplants grew less on the clearcut edge than they grew in the forest interior (7% vs. 12%, $p < 0.02$). The source of *P. rainierensis* thalli significantly affected transplant growth rate ($p < 0.02$). Specifically, thalli that came from the interior and were transplanted to the edge lost weight, on average, while thalli that came from the edge and were transplanted back to the edge grew an average of 10%.

WHAT'S SO SPECIAL ABOUT OLD-GROWTH FORESTS? AN EPIPHYTE'S PERSPECTIVE. Stephen C. Sillett and Peter N. Neitlich, Oregon State University, Corvallis.

Why do old-growth forests support such a diversity and abundance of cryptogamic epiphytes compared to younger forests? Answers to this important question may be found in the life histories of the cryptogams themselves. Epiphyte communities in young forests may be impoverished because of dispersal limitations and/or the unsuitability of canopy microhabitats for establishment and growth. Dispersal limitations are most evident when they are removed, such as in the rich epiphyte communities of young forests bordering old-growth. Young conifers may be a poor habitat for epiphyte growth compared to old conifers because microclimates within young tree crowns change rapidly with height growth, large horizontal branches are scarce, and dense crowns lead to low availability of light and direct precipitation. In contrast, hardwoods within young, conifer-dominated stands support a comparatively rich epiphyte flora. Large conifers in old-growth forests possess some of the structural attributes found in hardwoods, such as more open crowns and an abundance of large horizontal branch surfaces. Understanding the relative importance of dispersal, establishment, and habitat suitability for epiphytic cryptogams may be critical for the maintenance of late successional epiphytes within managed forests.

REPRODUCTIVE SUCCESS OF A RARE, RIPARIAN ORCHID. *Sedonia D. Sipes*, Utah State Univ., Logan. V. J. Tepedino, USDA Bee Biology and Systematics Lab, Utah State Univ., Logan.

We examined the breeding system and variations in reproductive success of Ute Ladies' Tresses, *Spiranthes diluvialis* Sheviak, a rare orchid from Colorado and Utah. *S. diluvialis* requires a pollen vector and exhibits a mixed-mating system. Outcrossing is promoted by protandrous flowers and by acropetal movement of long-tongued bees on inflorescences. Within plants, pollinia removal and fruit set were correlated. We found an inverse relationship between pollinia removal and both number of flowers per inflorescence and nearest neighbor distance. Neither of these characteristics were significantly correlated with fruit set. Rates of pollinia removal by bees varied greatly among five populations studied. We conclude that bumblebees are necessary for the reproduction of *S. diluvialis* and should be considered when making management decisions.

DIURNAL BEHAVIOR OF THE SPOTTED OWL IN WASHINGTON. Stan G. Sovern, Eric D. Forsman, Brian L. Biswell, Margaret Taylor, USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon. David N. Rolph, Seattle, Washington. Condor 96:200-202.

Northern spotted owls are primarily nocturnal, though some researchers have suggested that nesting spotted owls forage frequently during the day. Between May and September, 1989, we investigated the amount and types of diurnal behavior exhibited by spotted owls, including differences in diurnal activity based on reproductive status. We analyzed 346 prey remains from owl pellets to determine the proportion of diurnal prey in the diet. We recorded 4 categories of behavior during 96 observation hours: roosting, foraging, movement and social interaction. Nesting spotted owls spent significantly more time in active types of behavior and less time roosting than non-nesting owls. Owls were significantly more active after 18:00 hours. There was no significant difference in roosting versus active behaviors between males and females. Both nesting and non-nesting owls spent most of the day roosting and seldom traveled far from their roost sites. The proportion of diurnal prey in the diet was higher for nesting owls than for non-nesting owls, though not significantly so. We view diurnal foraging by spotted owls as an opportunistic response to the presence of prey, however, prey captured during the day are an important source of biomass.

SEASONAL DIET SHIFTS AND PREY AVAILABILITY IN A SHRUB-STEPPE BIRD COMMUNITY. Daniel A. Stephens, Wenatchee Valley College, Wenatchee, Washington.

Parameters of community organization were sought by analyzing the arthropod component of April and June diets (diet shift), and comparing these diet samples with three arthropod collections taken concurrently (prey availability). The study sites three dominant avian species, Brewer's Sparrow (*Spizella breweri*), Sage Thrasher (*Oreoscoptes montanus*), and Vesper Sparrow (*Poocetes gramineus*) were collected for stomach content analysis. A total of 90 stomachs were analyzed, comprising 3,036 arthropod prey items. Only the Brewer's Sparrow failed to show a positive correlation between April and June diets. The Sage Thrasher and Vesper Sparrow showed little diet shift. The strongest correlation of diet with prey availability was the Sage Thrasher with arthropod ground traps in April and June, the Brewer's Sparrow with brush beating in June, and the Vesper Sparrow with ground traps in April. The Sage Thrasher's affinity for ground foraging, the Brewer's Sparrow's affinity for foliage gleaning, and the Vesper Sparrow's lack of specialization suggests some structuring of the community based on feeding behavior. The Brewer's Sparrow's significant diet shift is probably due to greatly increased diversity of shrub arthropods from April to June, not a change in foraging behavior.

THE GEOMORPHIC HISTORY OF THE NORTHERN COLUMBIA PLATEAU. Dale E. Stradling and Eugene P. Kiver, Eastern Washington University. Cheney.

The nearly 200,000 km² of Miocene Columbia River Basalt was extruded from north-south trending fissures produced by east-west tension; whereas, north-south compression led to the forming of the Yakima Folds. Formation of the Blue Mountains anticline and basalt eruptions were contemporaneous. Upwarding and volcanism in the Cascades provided volcaniclastic debris which contributed to Columbia River Basalt interbeds and valley fill. Lesser amounts of low energy sediments derived from the Rocky Mountains contributed sediment along the northern and eastern Plateau boundaries. The Columbia, Snake and Yakima Rivers eroded canyons and watergaps accompanied by basin filling. Three major landscapes developed on the Columbia River Basalt during the Pleistocene. Reoccurring events produced the largely erosional Channeled Scabland, deposition of Lake Missoula flood sediments in the downstream basins and valleys and eolian deposition of loess.

SUPPRESSION OF TREE GROWTH WITH NITROGEN FERTILIZATION ON WESTERN WASHINGTON POWERLINE RIGHTS-OF-WAY. Angela B. Stringer and Stephen D. West, University of Washington, Seattle.

The use of ecological processes for controlling vegetation is becoming an important alternative to traditional chemical or mechanical means. An example of this is the manipulation of successional processes using limiting factors such as nitrogen. We analysed the response of vegetation to nitrogen after clearing in two demonstration projects designed to suppress tree growth on powerline rights-of-way. The first project used at 112 and 449 kg N/ha (urea) and resulted in a mixed grass and forb community. Tree regeneration was slowed but suppression was incomplete. The second project used 635 kg N/ha (biosolids) and resulted in a dense grass community. Tree suppression has been complete for 10 years. In both projects, the species richness of the plant community was lower and the regeneration time to tree establishment was longer than in control areas. We feel that such ecologically-based approaches warrant consideration in management programs.

TECHNIQUES FOR RADIO-TELEMETRY AND PIT-TAGGING OF SALAMANDERS. Angela B. Stringer, University of Washington, Seattle, Keith B. Aubry, USFS, PNW Research Station, Olympia.

Details of terrestrial movement patterns and distribution of Pacific Northwest salamanders are poorly known. We are conducting research on movements and habitat use of adult Northwestern salamanders (*Ambystoma gracile*) using radio-telemetry and pit-tagging. Small radio-transmitters (15x9x4mm) were surgically implanted into the peritoneal cavities of five large (>30g) salamanders. The salamanders were anaesthetized with a 0.5% solution of MS-222 and transmitters were inserted in a small incision on the side. We allowed the salamanders to recover for several weeks in the lab before release. The transmitters have a battery life of 4 months and a range of roughly 60 meters. The radio-transmitters will allow us to record daily and seasonal movement patterns including breeding migration. Pit-tags were implanted into Northwestern salamanders of all sizes using the same surgical procedure but with a smaller incision. Recovery was immediate. The pit-tags will allow us to identify salamanders for capture-recapture studies in their terrestrial habitat and at breeding ponds.

ENTRENCHMENT OF SMALL AND EPHEMERAL STREAMS IN ARID CENTRAL WASHINGTON STATE. Allen E. Sullivan, Central Washington University, Ellensburg.

Streams draining the shrub-steppe regions of central Washington State are generally small and ephemeral. Many of these streams are currently in a degraded condition that severely limits their utility to both fish and wildlife. A major component of this degradation is stream entrenchment. The timing of the entrenchment has been the subject of much discussion. Review of General Land Office survey maps and field notes, comparison of aerial photographs taken over several decades, and field reconnaissance of one stream, Johnson Creek in Kittitas County, support the conclusion that the entrenchment process is a recent, rapid, and continuing phenomenon.

THE BIOSYSTEMATICS OF BREWERS SPRUCE (*PICEA BREWERIANA*). Ronald J. Taylor and Steven Hahn, Western Washington University, Bellingham, WA.

The relationship of brewers spruce to other species of *Picea* of the United States and Mexico has been speculative. The large cones, weeping habit, flattened needles and general ecology suggest a close relationship to *Picea martinezii* of eastern Mexico and, to a lesser extent, *P. chihuahuana* of western Mexico. Needle shape, stomatal pattern and distribution suggest a relationship with *Picea sitchensis*. Alternatively, brewers spruce may have an independent origin from Asian ancestors. In this study, 20 plants from each of several populations of *Picea breweriana*, *P. martinezii*, *P. chihuahuana*, and *Picea sitchensis* were compared using taximetric methods involving 25 morphological and anatomical characteristics. The results of multivariate analyses (principal components and cluster analyses), based on the characteristics examined, brewers spruce is highly distinctive from the other species and is presumed to have been derived independently.

COMMERCIAL THINNING AND ALTERNATIVE TREE SPECIES REGENERATION TO ENHANCE SPECIES AND ARCHITECTURAL DIVERSITY IN YOUNG, MANAGED FORESTS. Ted B. Thomas and Andrew B. Carey, USDA Forest Service, PNW Research Station, Olympia, WA 98512-9193

Current silvicultural practices attempt to increase tree growth. Some new forestry is aimed at producing habitat for late-successional wildlife. Few attempt to address biodiversity, including plant species and architectural diversity of managed forest. A variable-density thin was implemented on 250 acres of *Pseudotsuga menziesii* forests on Fort Lewis, WA. The desired future condition would produce a matrix of high tree density and sparse understory with areas of low tree density and high vertical diversity of vegetation on a 2:1 ratio. Three additional conifer species (*Thuja plicata*, *Abies grandis*, *Pinus monticola*) and 1 hardwood (*Alnus rubra*) will be planted. Objectives are to accelerate understory development in areas of low tree density to fill the space between the crowns of overstory trees and tall shrubs, and increase species diversity including seed diversity, architectural diversity and associated mycorrhizal fungal diversity. The long-term contribution to both structural and functional diversity of these young forests will provide a suitable environment for foraging and roosting by the spotted owl and its primary prey, the flying squirrel.

RARE PLANTS OF SOUTH PUGET SOUND.

Ted Thomas and Andrew Carey

USDA Forest Service, PNW Research Station
Olympia, WA 98512-9193

Twenty plant species listed by the Washington Natural Heritage Program as endangered, threatened, or sensitive are suspected to occur on the glacial outwash soils of south Puget Sound. Four sensitive species—*Aster curtus*, *Trillium parviflorum*, *Carex comosa*, and *Carex interrupta* were found during systematic sampling for a plant diversity study. Over 7500 acres were surveyed on prairie, wetland and moist-forest plant communities. Species were mapped and their habitat and associated species described. *Aster curtus*, the most abundant sensitive species attained highest cover and frequency on prairies dominated by Idaho fescue, it was present on some sites dominated by alien species. *Trillium parviflorum* was found in moist-forest communities with overstories of conifers and hardwoods. Isolated patches of the two *Carex* species were found adjacent to wetlands (*C. comosa*) and on gravel bars of the Nisqually River (*C. interrupta*). Alien species invasion and encroachment by *Pseudotsuga menziesii* onto prairies have displaced native species. To insure the viability and restoration of sensitive plant species, management of rare plant habitat is recommended.

THE EVOLUTION OF SILVICULTURE ON FORT LEWIS MILITARY RESERVATION.

Ted Thomas, Andrew Carey, USDA Forest Service, PNW Research Station, Olympia, WA. and Gary McCausland and Jim Rohde, Environmental and Natural Resources Division, Fort Lewis, WA.

Fort Lewis, located in the Puget Sound lowlands, has practiced silviculture on 50,000 acres of managed forests for 50 years. Early practices included clearcutting and intermediate cutting with "stand cleanup" to promote tree growth. Subsequently, management practiced "multiple age rotations" to allow a continuous harvest of trees with partial overstory removal, and retention of coarse woody debris and defective trees valued for wildlife. In 1993, an experimental, variable-density thinning study was implemented on 300 acres of young Douglas-fir forests. The objective of the variable-density thinning study was to enhance plant and animal diversity, restore components of late-successional forests in managed stands, and improve forest health. Our objective here is to contrast these silvicultural approaches and the expected conditions each produces. Early management emphasized the output of timber with little regard to other resources. Current silviculture retains coarse woody debris as a component of sustained yield forestry. Our experimental study goals include enhancing biodiversity by thinning forests to provide habitat for late-successional wildlife species, to manage for a species-rich, structurally diverse forest, and to address forest health issues such as root-rot. Changes in forest management on Fort Lewis provide a model other agencies can follow in their journey to ecosystem management.

IDENTIFYING OREGON AMPHIBIANS IN THE FIELD: DISTINCTIONS BETWEEN LONG-TOED AND NORTHWESTERN SALAMANDERS. Chris Thoms and Charlotte C. Corkran, Northwest Ecological Research Institute, Portland, Oregon.

While preparing a manual for identifying live amphibians in the field in Oregon, observations of pond breeding salamanders were made in both field and laboratory from 1991 to the present. Distinctions between larval forms of Northwestern Salamanders (*Ambystoma gracile*) and Long-toed Salamanders (*A. macrodactylum*), and between reproductive habitats of these species were observed. Differences were noted in body proportions and gill structure of larval forms, in occurrence or non-occurrence of neotenic forms, and in the selection of oviposition sites. Maturation time (including occurrence of neotenic forms) and larval size appear to be directly related to reproductive habitat selection. A preliminary conclusion to be drawn from these observations is that Long-toed Salamanders can take advantage of temporary, shallow water habitats while Northwestern Salamanders are restricted to deeper, more permanent water situations. Thus it would appear that small temporary wetland can be as productive of one form of salamander as larger, more permanent and more obvious sites are of another.

INVASION OF PLANTS INTO ARTIFICIALLY CONSTRUCTED MICROSITES ON MOUNT ST. HELENS. Jon H. Titus and Roger del Moral, University of Washington, Seattle.

Twelve years after the eruption of Mount St. Helens, primary succession continues. To assess the influence of microsites on plant invasion patterns, 90 replicates each of these four microsite types were constructed; rocks, gullies, flat areas, and dead lupine patches. The Pumice Plain, a particularly barren area on the north side of Mount St. Helens, was the site of these studies. Plant invasion was recorded in 1992 and 1993. Microsites were invaded by 23 species, dominated by *Anaphalis margaritacea* and *Hypochaeris radicata*. More plants invaded microsites in 1993 than in 1992, perhaps due to site amelioration, seedbank development, and the moist summer. In 1992 plants invaded dead lupine microsites significantly more often than other microsites, however in 1993 there were no microsite preferences. Species varied in regards to which microsites they were most likely to invade. *Anaphalis margaritacea* invaded dead lupine sites more often than other sites in 1992, whereas in 1993 this species was more likely to invade gully microsites. *Epilobium angustifolium* and *E. alpinum* were each more common on dead lupine microsites in 1992 but showed no microsite preferences in 1993. *Hypochaeris radicata* was most likely to invade dead lupine microsites in 1992 but showed no differences between microsites in 1993. These results suggest that species differ somewhat in which microsites they are most likely to invade and that this microsite preference can fluctuate. Developing vegetation therefore may result from stochastic factors as well as dispersal and individual microsite preferences.

TANEUM CREEK WATERSHED ANALYSIS AND RESTORATION: AN EXAMPLE OF COOPERATIVE WATERSHED PLANNING. Steven E. Toth, Plum Creek Timber Co., Seattle, WA.

Watershed analysis is a biological and physical assessment of a watershed to address the cumulative effects of forest practices on public resources and is conducted by an interdisciplinary team of natural resource specialists. The Washington State *Standard Methodology for Conducting Watershed Analysis, Version 2.0* (developed by forest landowners, Native American tribes, environmental groups, and state natural resource agencies) was used to guide the analysis. Hillslope hazards are addressed by analysis of mass wasting, surface erosion, hydrology, and riparian condition. Resource vulnerabilities are examined in terms of fish habitat and channel condition. Sensitive areas are delineated and special prescriptions developed to address future management, restoration and monitoring. Most of the problems identified in the upper Taneum Creek watershed were a result of harvest in riparian areas and fine sediment from roads. Future land management in the basin will require larger buffers next to streams and a road improvement and maintenance plan to minimize sediment delivery to streams.

HISTORICAL AND CURRENT RUNS OF ANADROMOUS SALMONIDS IN THE YAKIMA RIVER BASIN, WASHINGTON. Bob Tuck, Ec Northwest, Selah, WA.

Prior to Euro-American development in the Yakima Basin, anadromous salmonid returns are estimated to have approached 1 million adults annually. By 1905, the returns had decreased to an estimated 50,000 adults annually. Although logging, grazing, minning, and other development activities bear some of the responsibility for this decline, it was the development of irrigated agriculture that was the primary cause of this decline. Today, the anadromous salmonid runs total less than 5,000 adults returning annually. Sockeye, summer chinook, and coho are extinct in the Yakima Basin. A petition for listing under the Endangered Species Act of 1973 has been filed on summer steelhead. The future of anadromous salmonids in the Yakima Basin depends upon modification of traditional water management practices that produce extreme low flows in the lower 100 miles of the Yakima River.

BUD-BREAK OF ADVANCED REGENERATION AS AN INDICATOR OF RESPONSE TO CANOPY GAP FORMATION. Robert Van Pelt, College of Forest Resources, University of Washington, Seattle.

Bud-break dates were collected on 979 understory trees in two 0.3 ha experimentally cut gaps to determine relative influences of competition and light during the springs of 1992 and 1993. An old-growth Douglas-fir/western hemlock forest at the Wind River Experimental Forest in the southern Gifford Pinchot National Forest was chosen for this study. Understory trees were 88% Pacific silver fir and 12% western hemlock. The gaps were cut in the winter of 1990-1991 with care to disturb the existing understory as little as possible. Bud-break dates were recorded every 3-5 days throughout the spring. Earliest date was May 3rd, 1992 and last date was June 15, 1993. Bud-break patterns indicate gap partitioning - trees breaking bud earliest in the north-central part of the opening, and latest in the south and/or under the canopy of the edge trees. This matches patterns of light and temperature within these gaps. Light and/or temperature was thus the dominant influence on the bud-break patterns, with (occasionally) strong influences from local competition.

CANOPY STRUCTURE IN FORESTS OF THE PACIFIC NORTHWEST. Robert Van Pelt and Malcolm P. North, University of Washington, Seattle.

Although the role of canopies in influencing forest ecosystem processes has long been recognized, little progress has been made in quantifying canopy structure. The scale at which researchers are interested in canopy attributes ranges from branches to whole landscapes. While canopy structure has often been inferred from measures of tree diameter or stand age, these measures are indirect and lack enough detail for quantitative analysis. Furthermore, analysis of three-dimensional canopy architecture is often based on two-dimensional measurements such as canopy projections. We propose a measure of canopy structure using simple, stand-level measures of individual crown dimensions. Canopy architecture can then be modelled and analyzed in three dimensions. Modelling allows prediction of understory light levels and the distribution of open space within complex canopies. These simple techniques provide an initial standard for future canopy research and a means of comparing canopy structure among different forest types.

DARK MATTER, MEDIUM FOR W-WAVES
O.E. Wagner, Wagner Research Lab.,
 Rogue River, OR 97537.

I previously reported W-Waves in plants (NWS '88, '89, '90). They appear to be waves that thread through everything, are illusive and interact very weakly (my work) with electromagnetic waves and other earthly fields. Nearly 99% of the universe is made of dark matter. I propose that waves in dark matter helped form and stabilize the solar system and organize plants so they can apparently defy the 2nd law of thermodynamics. If one sets the velocity expression for W-waves in space (see my book (1992) "W-Waves and a Wave Universe") equal to the reciprocal of the square root of the density of the medium then one finds that the density of the medium varies as the reciprocal of the square of the distance from the source (like the sun). This is just what one would expect for dark matter, demonstrating that the medium is dark matter. Dark matter would provide life with a stable and independent control medium. See Physics Today 45:28-36; 44:69-73; 46:22-29.

PLANT INTERACTION WITH 60 HZ. O.E. Wagner, Wagner Research Lab. Rogue River, OR 97537.

I measured many thousands of plant internodal spacings close to and far away from an electric power substation. I took distributions of these spacings converted to W-wave frequencies ($f=96/2s$, where s is a spacing in cm). Around 0.1 and 12 milligauss (ac magnetic field) spacings representing near 60 and 120 Hz appeared to occur less frequently. Intermediate values of ac magnetic field appeared to produce some clustering of spacings around 60 Hz, however. Field fluctuation during growing season produced ranges of ac electric and magnetic fields. Away from the substation I never observed the missing spacings in the open sunlight as I did in the substation fields. See book "W-waves and a Wave Universe". Spacings were from Ceanothus cuneatis, Rosa eglanteria, and Rubus Thyranthus. The results confirm the W-Wave hypothesis with W-wave and ac fields of similar frequency interacting weakly.

LANDSCAPE HABITAT USE BY FISHERS IN CENTRAL BRITISH COLUMBIA. Richard D. Weir, Simon Fraser University, Burnaby, B.C.

Habitat use by fishers (*Martes pennanti*) was examined on the landscape scale within the Sub-Boreal Spruce biogeoclimatic zone of British Columbia. Twenty-one fishers were radio-collared and followed for 2½ years. Habitat use patterns were determined comparing use to availability for all stand types within the study area. Habitat units were delineated by stands of homogeneous soil moisture and nutrient regimes, seral stage, slope position and plant associations. Fishers selected stands with wetter moisture regimes, and avoided cutblocks and natural habitats with little canopy cover. Fishers also selected stands with above average volumes of coarse woody debris. Fishers appear to select older seral stage habitats and habitats within or immediately adjacent to wet areas.

THE DEMOGRAPHY AND POPULATION DYNAMICS OF CASTILLEJA LEVISECTA, AN ENDANGERED PERENNIAL. Jane B. Wentworth, University of Washington, Seattle.

Population dynamics of *Castilleja levisecta*, an endangered, hemiparasitic perennial, were examined by constructing stage-structured transition matrix models. The models were based upon life history parameters obtained from three years of empirical data from two study plots. The purpose of the study was to examine 1) basic demographic parameters such as growth, survival, and reproduction, 2) population growth rate and associated stable-stage distribution and reproductive values, and 3) demographic sensitivities within a given environment. Observed stage distributions varied among plots and years. The number of reproductive individuals decreased by 85% in Plot 1 and increased by 56% in Plot 2 from 1991-1993. The population is characterized by prolific seed production (mean = 1959 seeds per plant), limited seedling recruitment, the ability for small plants to grow quickly within a single season, and for large plants to shrink rather than die. Population growth rates, given by the dominant eigenvalue of the matrices, or λ , indicate that population growth for this plant is variable within a relatively short time period.

DISTRIBUTION OF VAN DYKE'S SALAMANDER (*PLETHODON VANDYKEI*). Albert G. Wilson, Jr., Washington State University, Pullman. Kelly R. McAllister, Washington Department of Wildlife, Olympia. John H. Larsen, Jr., Washington State University, Pullman.

Literature and field surveys were conducted to document occurrence of *Plethodon vandykei*, an amphibian endemic to Washington State. The distribution of *P. vandykei* was compared cartographically with Pacific Northwest climatic and geologic variables to reveal possible limiting factors and regions potentially inhabited by the salamander. Field surveys did not appreciably expand the known range of *P. vandykei*, which has been collected from three disjunct centers of distribution in the southern Cascade Range, the Willapa Hills, and on the Olympic Peninsula. These centers are separated by glacial and alluvial deposits in the Puget Trough and coastal lowlands which may historically have restricted occurrence by the salamander except during development of closed mesophytic forests.

TRAP PLACEMENT AND INTERPRETATION OF HABITAT USE PATTERNS IN FOREST FLOOR SMALL MAMMALS. Suzanne M. Wilson and Andrew B. Carey, Pacific Northwest Research Station, USDA Forest Service, Olympia, WA.

We consider the effects of annual population variation, habitat use patterns, and relict populations on the structure of two small mammal communities. Through trap placement we tested whether habitat features are preferentially used or avoided by forest floor small mammals. Chi-square analysis of capture data, from the Fort Lewis Military Reservation, show that traps placed among understory shrubs had higher than expected capture rates of *Peromyscus maniculatus*. *Sorex monticolus* showed a positive response to traps placed adjacent to coarse woody debris and decay-class-v-logs and a negative response to traps placed in the open or at the base of large trees. The magnitude of annual variation in captures was not the same among species. Abundance measures for insectivores were similar between years but in 1993 *Peromyscus maniculatus* were significantly less abundant than during 1992. Small, possibly relict, populations of *Peromyscus oreas* occur in both communities.

DEN SITES OF *GLAUCOMYS SABRINUS* IN THE PACIFIC NORTHWEST. Todd M. Wilson and Andrew B. Carey, USDA, Pacific Northwest Research Station, 3625 93rd Ave., SW, Olympia, WA 98512

The northern flying squirrel is an important ecological component of Pacific Northwest forests, yet very little information is known about their diurnal dens. We located 501 dens from 1986 to 1993: 98 in old-growth stands and 12 in young stands in the Coast Range of Oregon; 10 in young stands in the Olympic Mountains of Washington; and 381 dens in two young forests (unthinned and intensively managed) in the Puget Trough of Washington. Live trees accounted for 2/3 of the den structures in both old-growth and young stands. Snags comprised the remaining 1/3 except low structures (stumps, fallen trees, and rootwads) accounted for 6% of the dens in the Puget Trough and were used exclusively by females in May and June. There was a higher percentage of exterior dens (twig, moss, and/or leaf) in unthinned stands (57%) than in managed stands (40%) in the Puget Trough. Den types were difficult to detect in large live trees. Types of dens used often mimicked den site availability. Stand history may play an important role in determining den site use by flying squirrels.

WEASELS: UNDERRATED PREDATORS OF NORTHWEST FORESTS. Todd M. Wilson and Andrew B. Carey, USDA, Pacific Northwest Research Station, 3625 93rd Ave., SW, Olympia, WA 98512

Much of the recent focus in Northwest forests has been on charismatic metafauna such as owls, grizzly bears, and marten. Small mammalian predators, especially weasels, have often gone unnoticed, yet their importance in Northwest ecosystems may be just as significant. Live-trapping studies for arboreal and forest floor small mammals were conducted from 1986-1993 in conifer forests of western Oregon and western Washington. Few long-tailed weasels (*Mustela frenata*) and ermines (*Mustela erminea*) were captured. However, records of predator-killed rodents in traps and visual observations show the presence of weasels in some of the forest stands and suggest different densities. Radio-telemetry studies of flying squirrels in young forests in the Puget Trough indicate that weasels are the primary predator of flying squirrels in some stands. Circumstantial evidence to date clearly shows a need for further investigation into the role weasels play in Northwest forests.

CENTINELAN EXTINCTIONS: EXTIRPATION OF NORTHERN TEMPERATE OLD-GROWTH ARTHROPOD COMMUNITIES. Neville N. Winchester, University of Victoria, Victoria, British Columbia

Arthropod biodiversity is being investigated in the Carmanah Valley on Vancouver Island, B.C. Examination of several species, many of which are not yet described from this intact old-growth forest indicate that this structurally complex habitat acts as a reservoir for biological diversity. Nowhere is this more apparent than in the canopy, where the fauna has finely partitioned the tree, both with regard to habitat type and phenology. Microhabitats exploited by this arboreal arthropod fauna are not replicated in any of the other forest sites that we examined. That these species form a taxonomically discrete epiphytic community clearly demonstrates that removal of this habitat will forever change the structural and functional aspects of these ecosystems and initiate species extinctions.

THE PROTECTION OF RESEARCH PERSONNEL, EQUIPMENT, AND DATA. Gary W. Witmer, USDA/APHIS/DWRC, Washington State University, Pullman. Bex O. Baker, California State Polytechnic University, Pomona.

Wildlife field research is important, conducted for various reasons, and often difficult work. Researchers must have state and federal permits and abide by various state and federal laws. The work must be approved by an Animal Care and Use Committee and meet requirements of the Animal Welfare Act. Despite this careful regulation, there have been attempts in recent years to disrupt legitimate research. Researchers have been subjected to harassment and threats, burglaries, fire bombings, and equipment vandalism or theft. Federal legislation, The Animal Enterprise Protection Act of 1992, makes such acts illegal and the persons involved subject to fines or incarceration. Researchers can help protect personnel, equipment, and data by: having paperwork and approvals in order and doing things in an approved manner in the field; informing appropriate agencies of their activities; educating themselves to the hazards and protective measures; developing a public relations program; following basic security procedures at buildings, pens, labs, and offices; screening potential employees and media personnel; conducting interviews away from research sites or facilities; providing radio communication between field personnel; avoiding confrontations with disruptive persons; changing research "modus operandi" periodically; and keeping a copy of data, files, and computer disks at a secondary location.

RESEARCH ON NONLETHAL METHODS OF POCKET GOPHER (*THOMOMYS* spp.) DAMAGE MANAGEMENT. Gary W. Witmer, USDA/APHIS/DWRC, Washington State University, Pullman. Dan Campbell, USDA/APHIS/DWRC Olympia.

Nonlethal methods to reduce gopher damage to conifer seedlings are being tested, including repellents, physical barriers, and habitat modification. Denatonium benzoate (DB), a bitter compound, was applied to seedlings on Mt. Hood Nat'l Forest (NF) in OR. In the results of preliminary trials with DB, seedling damage and mortality was 44% (controls), 38% (DB tablets placed in roots at planting), and 31% (DB tablet plus DB spray). A problem may be poor systemic uptake by plants undergoing moisture stress. Physical barriers around seedling roots and tops has helped reduce initial seedling damage and mortality at Mt. Hood NF. Losses of control seedlings after 6 months to gophers was 55%, but only 23% to seedlings wrapped in heavier weight plastic mesh tubes, 26% in lighter weight plastic mesh tubes, and 11% in sandpaper tubes. The sandpaper tubed seedlings, however, heavy non-animal mortality (>90%) from constriction or heat build up. Habitat modification by sheep grazing is being tested in southcentral WA for its ability to reduce gopher populations. Sheep are used to reduce vegetation on clearcuts and shelterwood units that competes with conifer seedlings. Gopher densities were high (~9-10 gophers/acre) for exclosures (no grazing) and cattle-grazed areas; whereas densities were considerably lower (~3/acre) on areas intensively grazed by sheep.

RESOLVING CARNIVORE-HUMAN CONFLICTS. Gary W. Witmer, USDA/APHIS/DWRC, Washington State University, Pullman. J. Gary Oldenburg, USDA/APHIS/ADC, Olympia.

Carnivores are important components of forest ecosystems. There have been many efforts to re-establish populations or better manage existing populations. Conflicts can occur when human life or property is threatened or damaged (e.g., persons, pets, livestock), important game populations are impacted (e.g., big game, upland game, waterfowl), or threatened or endangered species are affected (e.g., Columbia white-tailed deer, snowy plover, CA least tern, sandhill and whooping cranes, kit foxes, native Hawaiian birds). Problems often occur when carnivore densities are high and they have largely lost their fear of humans and human habitations. This has resulted in occasional control of carnivores, including wolves, coyotes, foxes, mountain lions, bears, raccoons and skunks. Before action is initiated, the problem species must be identified; the location extent, and timing of the problem understood; and the various control options considered. Management programs should be tailored to the local situation and the individuals causing the damage. Conflict resolution is often hampered by the secretive and elusive nature of carnivores and the remote rugged forestlands that they can inhabit. A variety of methods, both lethal and nonlethal, are available for aiding in conflict resolutions. Multiple methods and the principles of integrated pest management should be incorporated into the management programs. Additional or improved methods that are effective, practical, legal, and socially acceptable, are needed.

SEX-BIASED NATAL DISPERSAL IN MAMMALS. Jerry O. Wolff, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, 97331, USA

I present a conceptual model to explain sex-biased natal dispersal in mammals based on adaptive strategies of parents, offspring, and nonrelatives. Dispersal involves emigration from the natal site, transience, and immigration to a new home range. Emigration should be voluntary and function to avoid inbreeding, whereas immigration may involve aggression associated with resource and/or reproductive competition. The "cost" of dispersal may be over-estimated and less relevant to dispersal than most models predict. Male-biased dispersal is a consequence of female philopatry, female philopatry being a consequence of fathers with short reproductive lifespans. Dispersal distance varies by sex and what is being defended, space or mates. Delayed dispersal occurs in saturated habitats and may result in delayed maturation, cooperative breeding, or communal nesting depending on the presence or absence of opposite-sex relatives.

ESTABLISHMENT OF TREES IN SUBALPINE MEADOWS OF OLYMPIC NATIONAL PARK. A. Woodward University of Washington, Seattle, E. G. Schreiner, Olympic National Park, Port Angeles, and D. G. Silsbee, University of Washington, Seattle.

Establishment of trees in subalpine meadows may be a response to changing climate in the twentieth century. We aged young trees in meadows at 6 sites representing 3 points on a precipitation gradient in Olympic National Park. We found that climatic conditions favoring establishment vary with region and tree species. Specifically, establishment occurred in dry areas with wetter conditions, and in wet areas with drying. Mountain hemlock established in warmer and drier conditions than silver fir. Establishment of subalpine fir was associated with increased winter precipitation. We conclude that autecology of trees is more important than specific climate variables for predicting change.

MERRIAM'S SHREW AND SMALL MAMMAL COMMUNITIES ON THE YAKIMA TRAINING CENTER, WA. Laurie Wunder and Andrew B. Carey, Pacific Northwest Research Station, Olympia, WA.

Merriam's shrew (*Sorex merriami*) is known to be closely associated with shrub-steppe environments. With the widespread decline in this habitat type, concern has focused on those species which might be most affected by the decline, including Merriam's shrew. This study was undertaken in conjunction with the Department of the Army, Ft. Lewis, in order to assess relative abundance and habitat associations of Merriam's shrew on the Department of the Army's Yakima Training Center, located in central Washington. Shrews and other small mammals were live-trapped using Sherman live-traps and pitfall traps, set out on 3.24 ha grids in 3 habitat types. Deer mice (*Peromyscus maniculatus*) and sagebrush voles (*Lemmus curtatus*) made up the greatest percentage of captures (62% and 24%, respectively). Merriam's shrew were found to make up only 2% of total captures. Merriam's shrew was widely distributed across all habitats sampled. Although densities of this shrew appear to be low, it may be more abundant in central Washington than previously thought.

USE OF THE FOREST CANOPY BY BATS. Laurie Wunder and Andrew B. Carey, Pacific Northwest Research Station, Olympia, WA.

Some 10 species of Pacific Northwest bats are known to make regular use of the forest canopy for day or night roosting, foraging, hibernation and/or reproduction. An additional 4 species may occasionally be found roosting or foraging in the forest canopy. In this paper we discuss roosting requirements, foraging strategy, community structure, and the importance of landscape level factors, such as proximity to water, for species occurring both east and west of the Cascade Mountains. Both coniferous and hardwood forests are considered and compared. The role of bats in forest ecosystems is examined. A brief summary and comparison of bat forest canopy communities elsewhere in the world, is also presented.

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Agricultural Development and Its Influence on Raptors in Southern Idaho

Abstract

The U.S. Bureau of Reclamation has proposed an extension of their North Side Pumping Diversion in Minidoka and Jerome counties, Idaho. The project would result in 3885 ha of rangeland being converted to irrigated agricultural production. This study examined the influence of agricultural development on raptor abundance and diversity on the project area. Road surveys for raptors were conducted through a mix of agricultural and range land in 1986 and 1987. Eleven species of raptors were recorded during observations along 780 km of road surveys. Raptors were significantly more abundant on land that was not highly developed for agriculture in all seasons except the fall migration, when abundance was equal between agricultural and range lands. Raptor diversity varied by season and was higher on undeveloped lands during summer and fall migration. Most raptor species observed made some use of agricultural lands and species richness was similar for both the agricultural and rangeland types. However, species distribution on developed lands was skewed towards a few species that tolerated agricultural development well. Individual species responded differently to conversion of native rangelands to irrigated agricultural production. As a community, raptors exhibited decreased abundance and lower diversity in areas highly developed to irrigated agriculture.

Introduction

Thousands of acres of native western rangelands have been converted to irrigated cropland in the intermountain west. Raptor response to agricultural development has been studied in the more mesic habitats of the Great Plains (Schnell 1968, Gilmer and Stewart 1983, Schmutz 1984). Although some work has been done on nest site selection (Howard *et al.* 1976, Howard and Sather-Blair 1983, Rich 1986), little is known about the effects of agricultural development on raptors using the dryer rangeland habitats of the intermountain region. This study was done in connection with the United States Bureau of Reclamation's proposed extension of the North Side Pumping Diversion. Under the recommended development plan, approximately 3885 ha of rangeland vegetation would be converted to irrigated agricultural production. This study examined the effects of agricultural development on raptor abundance and diversity in the project area.

Study Area

The study area was located in the shrub-steppe/grassland zone (Davis 1952) of the Snake River Plain north of U.S. Interstate 84 in eastern Jerome and western Minidoka counties, Idaho (U.S. Bureau of Reclamation 1986). Vegetation consisted of shrub-steppe and grasslands interspersed through irrigated farmland. Major agricultural crops were alfalfa, barley, wheat, dry beans, corn, potatoes, and sugar beets. Rangeland grasses were dominated by cheatgrass (*Bromus tectorum*), Sandberg's bluegrass (*Poa sandbergii*), blue bunch

wheatgrass (*Agropyron spicatum*), and squirrel tail (*Sitanion hystrix*). Big sagebrush (*Artemesia tridentata*), and rabbit brush (*Chrysothamnus spp.*) were the dominant shrubs.

Topography of the area was gently rolling with elevation varying from 1230 m near the Snake River in the south to 1540 m in the north. Annual precipitation averaged 23 cm.

Methods

Field work was conducted from June 1986 to May 1987. Road surveys were conducted twice a month, at about two week intervals, along a 32.5 km census route through a mixture of agricultural land and undeveloped rangeland. Survey data were collected by one or two observers. The same primary observer was present on all surveys and only two different secondary observers were used. Observers scanned out to 400 m on both sides of the road while traveling at speeds of 8-24 km/hour. The number of observers was not considered an important factor in data collection. Travel speed was adjusted to ensure a thorough count was obtained and all surveys were treated equally in the analysis. When a raptor was spotted the vehicle was stopped, a positive species identification was made, and species and transect segment were recorded. Surveys began between 0800 and 0900 hours and lasted 2.5 to 4.0 hours. Successive surveys were conducted in opposite directions to reduce any time bias. Binoculars and a 15-60 variable power spotting scope were used when identifying raptors. Seasons were defined by julian

dates as summer (152-212), migration (213-258), fall (259-334), winter (335-74), and spring (75-151).

The survey route was divided into 20, 1.6 km segments. At 160 m intervals, the amount of agricultural and rangeland in each segment was subjectively determined in a 400 m strip on both sides of the road. This resulted in 20 (10, 160 m intervals x 2 sides of the road) cover classifications for each 1.6 km segment. The resulting classifications were summed to determine the proportions of rangeland and agricultural land in each segment. Segment composition varied from 100% rangeland vegetation to 100% agricultural crops. Eleven segments were $\geq 50\%$ developed to agriculture (developed) and averaged only 24% rangeland vegetation. Nine remaining segments were $\leq 50\%$ developed to agriculture (undeveloped) and averaged 75% rangeland vegetation. These two groups were used to examine the effect of agricultural development on the raptor community.

An index of seasonal abundance of raptors was calculated as no. birds/100 km of road survey. A G-test (Sokal and Rohlf 1981) on frequency of occurrence was performed to compare raptor abundance on developed and undeveloped land. I tested for independence of raptor distribution and segment type using chi-square analysis (Sokal and Rohlf 1981). A Bonferroni Z statistic was used to identify how the four most common summer and winter resident raptors species (comprising 74% of all observations in both seasons) used developed and undeveloped survey segments relative to what was expected from their availability (Nue *et al.* 1974). Diversity of the raptor community was calculated using the Shannon-Weaver function and Pielou's equitability index (Hair 1980). Differences in diversity were examined using the Hutcheson t-test (Zar 1984).

Results

Eleven species of raptors were recorded during observations along 780 km of road surveys (Table 1). During migration a group of 127 Swainson's hawks (*Buteo swainsoni*) were seen circling a freshly cut hay field. I considered this an outlier observation and it was excluded from all analyses. Overall, raptor abundance was lowest during the winter, increased through spring and summer, reached its peak at fall migration, and declined through the fall to winter levels.

Raptors were significantly more abundant ($P < 0.01$; $G = 28.28, 11.8, 7.40, 9.36$; d.f. = 1; respectively for summer, fall, winter, and spring) on the undeveloped segments during all seasons except the fall migration when densities were equal ($P > 0.25$; $G = 0.2$; d.f. = 1).

Raptor species did not use developed and undeveloped segments in proportion to their availability during any season, including fall migration when raptor densities were not different between segment types ($P < 0.01$; $X^2 = 46.01$, d.f. = 6; $X^2 = 35.99$, d.f. = 7; $X^2 = 25.95$, d.f. = 6; $X^2 = 28.25$, d.f. = 7; $X^2 = 21.35$, d.f. = 6; for summer, fall migration, fall, winter, and spring respectively). During summer red-tailed (*Buteo jamaicensis*) and Swainson's hawks ($P < 0.05$) and northern harriers (*Circus cyaneus*) ($P < 0.1$) used undeveloped segments more than expected, while burrowing owls (*Speotyto cunicularia*) used developed segments more than expected ($P < 0.05$). During winter northern harriers and prairie falcons (*Falco mexicanus*) used undeveloped segments more than expected from availability ($P < 0.05$). Red-tailed and rough-legged (*Buteo lagopus*) hawks used segments in proportion to their availability ($P > 0.1$).

Diversity varied among seasons. Summer and winter were the seasons of greatest raptor diversity while fall migration was the season of lowest raptor diversity (Table 2). Within seasons species diversity was higher on undeveloped segments during summer and fall migration ($P < 0.05$; $t = 2.31$, d.f. = 83; $t = 3.07$, d.f. = 312, respectively) and equal during fall, winter and spring ($P > 0.1$; $t = 1.41$, d.f. = 124; $t = 1.59$, d.f. = 80; $t = 1.54$, d.f. = 88, respectively).

Discussion

An implicit assumption of the road survey technique is equal sightability of raptors among both species and cover types. However, differences in the size and behavior of species as well as vegetation structure result in differences in detectability among species (Millsap and Le Franc 1988). Caution should be used in comparing relative abundance among different species.

The burrowing owl was the only major resident species to demonstrate an affinity for highly developed sites. This association of burrowing owls with cultivated land has been previously documented in southern Idaho (Rich 1986). My

TABLE 1. Seasonal relative abundance of Minidoka project extension land raptors on land developed for agriculture, undeveloped, and all survey segments combined, expressed as birds/100 km of survey.

	Season														
	Dev.	Summer N=4 Und.	Comb.	Dev.	Migration N=3 Und.	Comb.	Dev.	Fall N=5 Und.	Comb.	Dev.	Winter N=7 Und.	Comb.	Dev.	Spring N=5 Und.	Comb.
Burrowing Owl	20.98	6.84	14.62	5.59	4.56	5.14	0.00	0.00	0.00	0.00	0.00	0.00	11.19	28.72	19.08
Ferruginous Hawk	0.00	0.00	0.00	1.86	2.28	2.06	0.00	1.37	0.62	0.00	0.98	0.44	0.00	0.00	0.00
Golden Eagle	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.74	1.23	2.40	7.81	4.83	0.00	0.00	0.00
Kestrel	4.20	10.26	6.92	11.19	15.95	12.31	3.36	8.21	5.54	4.80	1.98	3.51	5.59	8.21	6.77
Northern Harrier	13.99	32.48	22.31	27.97	31.91	29.75	11.19	23.25	16.62	0.80	12.70	6.15	5.59	8.21	6.77
Merlin	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.80	0.00	0.43	0.00	0.00	0.00
Prairie Falcon	0.00	1.71	0.77	3.73	4.56	4.09	3.36	6.84	4.92	3.20	12.70	7.48	1.12	2.74	1.85
Red-tailed Hawk	2.80	37.61	18.46	20.51	84.33	49.23	19.02	41.03	28.92	5.59	8.79	6.58	1.12	2.74	1.85
Rough-legged Hawk	0.00	0.00	0.00	0.00	0.00	0.00	10.07	31.45	19.69	15.98	21.49	18.89	4.48	25.98	14.15
Short-eared Owl	5.59	11.97	8.46	0.00	2.28	1.02	0.00	0.00	0.00	0.00	0.00	0.00	4.48	4.10	4.31
Swainson's Hawk	1.40	22.22	10.77	264.80	25.07	215.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Unidentified	0.00	13.68	6.15	39.16	43.30	42.06	6.71	9.57	8.00	2.40	6.84	4.40	8.95	1.37	5.54
Total	48.96	136.77	88.46	374.81	214.24	364.09	53.71	124.46	85.54	35.97	73.28	52.74	42.52	82.07	60.31

1. N = the number of 32.5 km surveys conducted during that season.

TABLE 2. Summary of raptor diversity indices on developed and undeveloped land and both types combined reported by season.

Season ¹	Undeveloped			Developed			Combined		
	Number Species	H'	J'	Number Species	H'	J'	Number Species	H'	J'
Summer _a	7	1.6764	0.8615	6	1.4585	0.8140	7	1.7480	0.8983
Migration	7	1.2821	0.6589	7	0.8255	0.4240	8	1.0672	0.5132
Fall _b	7	1.5438	0.7933	5	1.4148	0.7271	7	1.5126	0.7779
Winter _{a, b}	7	1.6829	0.8648	7	1.5202	0.7812	8	1.7054	0.8201
Spring _{a, b}	7	1.5785	0.8112	7	1.7278	0.8879	7	1.6627	0.8544

1. Diversity indices of seasons subscripted by the same letter were not different ($P < 0.05$).

findings indicated that the other major summer and winter resident raptor species are less abundant on lands highly developed to agriculture. In Idaho, Howard and Sather-Blair (1983) studied two raptor communities along the Snake river canyon and found significantly lower nest densities in agricultural habitat. They concluded that lower prey densities in agricultural areas were responsible for the difference in raptor nesting densities. Howard *et al.* (1976) inventoried nesting raptors at seven sites in southern Idaho. They also noted that nesting density varied with prey abundance. On my study area Kessler (1979) found the relative abundance of small mammals on rangelands was greater than on dry and irrigated farmland. Prey densities may help to explain the difference in the abundance of raptors between developed and undeveloped segments.

Significant reductions in the abundance of raptors on agricultural land have been reported in other areas of North America. Schnell (1968) reported decreased use of intensively cultivated land by red-tailed and rough-legged hawks during the winter in the midwest. Nesting density of ferruginous (*Buteo regalis*), but not Swainson's hawks, declined with increasing percentages of the landscape under cultivation in southeast Alberta and North Dakota (Gilmer and Stewart 1983, Schmutz 1984).

The undeveloped survey segments included one more species during summer than the developed segments due to a single observation of a prairie falcon. Although this observation did contribute to the significantly higher H' value on the undeveloped habitat, a more even distribution of species was responsible for most of the difference. This

was born out by the higher J' value for the undeveloped segments. Similarly, during fall migration both segment types had the same number of species. Differences in evenness of species distribution were entirely responsible for differences in diversity. It appeared that most raptors in this area made some use of agricultural land and that species richness on developed and undeveloped land was similar. However, species distribution on developed land was more skewed toward a few species that tolerate agricultural development well.

Seasonal changes in diversity showed fall migration was the time of lowest diversity regardless of the fact that species richness was as great or greater than in other seasons. The low H' value was due to the large number of Swainson's hawks in the raptor community at this time. Migrating Swainson's hawks represented only 12.5% of the species but accounted for 60% of the observations during this season. This unevenness was the primary reason for the low diversity index. The pattern of highest diversity during winter and summer with reduced diversity during spring and fall may reflect a temporary perturbation to the community during the transition between summer and winter residents.

Some of the variation in raptor responses to agricultural development might be attributed to over-simplification of the cover type classifications. Row crops, cereal grains, and hay were all combined into the agricultural type but they almost certainly influence raptor abundance in different ways. Similarly, rangelands included both grasslands and shrublands which experienced varying degrees of grazing. Working on the same study area Leptich (1987) reported small mammal abundance in rangeland habitats was reduced by grazing.

Differences in vegetation structure and small mammal prey bases were additional contributors to variability in raptor responses within types. Regardless of this variation, the results suggest that the current mix of agricultural crops does result in decreased raptor abundance and diversity. This is probably modified by crop composition which in turn is influenced by the agricultural economy.

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Furthermore, rangelands on the study area are recognized as being in generally poor condition as a result of overgrazing (U.S. Bureau of Reclamation 1986). Had these lands provided higher quality habitat, it is possible that the disparity in abundance and diversity between developed and undeveloped lands would have been even greater.

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Winter Diet and Weights of Barrow's and Common Goldeneye in Southcentral Washington

Abstract

Little data are available relative to diets and body weight dynamics of wintering Barrow's and common goldeneyes in freshwater habitats, and no data exist for subadults. Diets of these birds were studied on the Columbia and Yakima Rivers in southcentral Washington from October through May 1955-1956 and 1956-1957. Trichopteran larvae accounted for more than 67% of common goldeneye and 81% of Barrow's goldeneye food biomass. Mollusc and aquatic plant achenes were other important food items. Average weights of common goldeneye ranged from 599.3 ± 39.86 g for subadult females to 1060.2 ± 33.36 g for adult males. Average weights of Barrow's goldeneye ranged from 736.0 ± 44.73 g for subadult females to 1330.5 ± 18.69 g for adult males. Body-weight dynamics of birds may reflect resource availability, competition, and bioenergetics, all of which may influence winter distribution, differential migration and habitat use by sexes.

Introduction

The Hanford Reach of the Columbia River and a tributary, the Yakima River (Figure 1), are important wintering habitats for both Barrow's goldeneye (*Bucephala islandica*) and common goldeneye (*B. clangula*) (Yocom 1951, Fitzner and Rickard 1975). The mallard (*Anas platyrhynchos*), northern pintail (*A. acuta*), American wigeon (*A. americana*), green-winged teal (*A. crecca*), ring-necked duck (*Aythya collaris*), canvasback (*A. valisineria*), redhead (*A. americana*), lesser scaup (*A. affinis*), greater scaup (*A. marila*), and bufflehead (*Bucephala albeola*) ducks share the Columbia River with goldeneyes.

The Columbia River remains open throughout the winter while the Yakima River sometimes freezes over. However, rapids on the Yakima River remain open even during the coldest periods, providing feeding areas for goldeneyes and other ducks. The Hanford Reach, a 90-km stretch, is currently the only remaining segment of the Columbia River in the United States not impounded by hydroelectric dams. Proposals to construct Ben Franklin Dam and build a barge shipping channel through the Hanford Reach have threatened to modify this segment of river. Demands have already been made on the waters of both rivers through irrigation withdrawal. In addition, return runoff contains agricultural chemicals that could alter the aquatic fauna of these rivers. A new proposal to classify the Hanford Reach as a wild and

scenic river is now being reviewed. Currently, there is little information available to develop effective management plans or assess the effects of human activities on waterfowl wintering habitat along the Columbia and adjoining Yakima rivers.

Winter diets of common and Barrow's goldeneyes were studied from 1981 through 1988 to better understand the food requirements of these species during a stressful period of their annual cycle. This information is needed to effectively develop waterfowl management plans for the Columbia and Yakima rivers.

Methods

We collected 39 Barrow's goldeneye and 33 common goldeneye that were shot by hunters during October through May, 1955 through 1957. The esophagus and proventriculus were removed and their fresh contents separated, identified, and weighed to within 1 g (to within 0.1 g if less than 1 g) to determine percent wet weight and relative frequency of food items. Body weights were also recorded to the nearest gram. Plant food items were identified using Scheffer and Hotchkiss (1945).

Results and Discussion

Food Habits

All but one bird, a subadult female common goldeneye, contained food items. Aquatic insects composed 86% (wet weight) of the common goldeneye diet (Table 1). Two trichopteran larvae, *Brachycentrus* sp. and *Hydropsyche cocherelli*, accounted for

¹To whom correspondence should be addressed:
Environmental Protection, Battelle Pantex, P.O. Box 30020,
Amarillo, TX 79177

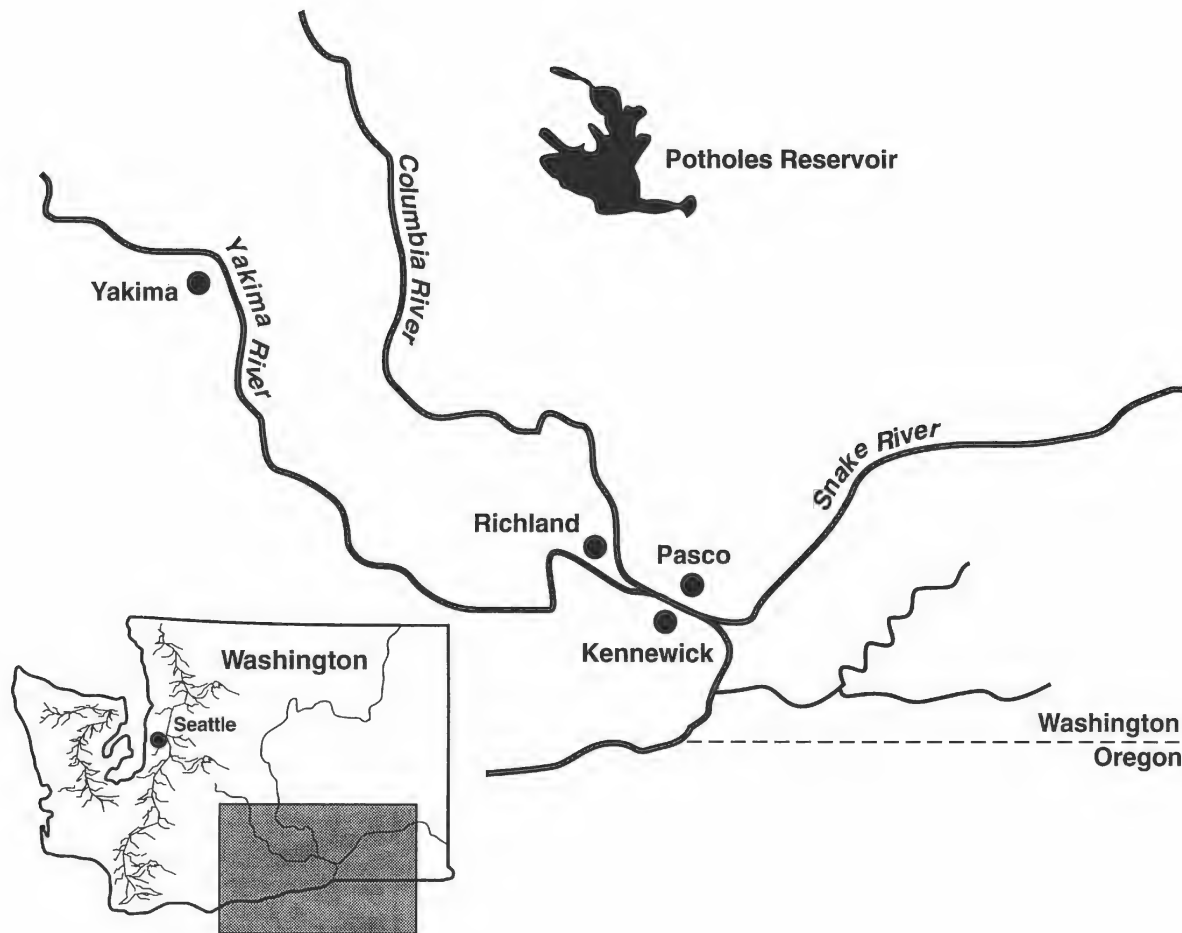


Figure 1. Columbia and Yakima rivers in southcentral Washington.

TABLE 1. Food items in common goldeneye collected on the Yakima and Columbia rivers, Southcentral Washington, 1955-1957

Taxa	Average Weight Per Bird	Total Wet Weight (g)	% Total
Plant Matter			
unidentified vegetation	0.7	24.0	1.00
<i>Echinochloa crus-gali</i> achenes	0.5	16.0	0.43
<i>Potamogeton pectinatus</i> achenes	0.3	11.0	0.30
<i>P. foliosius</i> achenes	0.1	2.0	0.05
<i>Polygonum natans</i> vegetation	0.3	10.0	0.27
<i>P. hydropiper</i> achenes	1.0	32.0	1.00
<i>P. lapathifolium</i> achenes	1.2	38.0	1.00
<i>Scirpus acutus</i> achenes	0.6	20.0	1.00
<i>S. americanus</i> achenes	0.2	7.0	0.19
<i>S. paludosus</i> achenes	0.03	1.0	0.03
<i>S. nevadensis</i> achenes	0.2	5.0	0.13
<i>Eragrostis megastocha</i> achenes	0.1	3.0	0.08
Total Plant Matter	5.23	169.0	5.00
Animal Matter			
Crustacea			
<i>Pacifastacus</i> sp.	0.1	3.0	0.08
Insecta			
unidentified larvae	16.0	540.0	15.00
Coleoptera adults	1.4	45.0	1.00
Corixidae adults	1.2	41.0	1.00
Notonectidae adults	0.03	1.0	0.03
Odonata naids	1.5	50.0	1.00
unidentified ephemeroptera naids	1.5	50.0	1.00
<i>Brachycentrus occidentalis</i> larvae	60.0	1981.0	53.00
<i>Hydropsyche cocherelli</i> larvae	14.0	464.0	12.00
<i>Cheumatopsyche campyla</i> larvae	1.4	46.0	1.00
Total Insecta	97.03	3218.0	86.00
Gastropoda			
<i>Fisherola nuttalli</i>	4.1	136.0	4.00
<i>Fluminicola columbiana</i>	1.1	149.0	4.00
<i>Gyraulus</i> spp.	0.1	4.0	0.11
<i>Stagnicola apicina</i>	1.1	37.0	1.10
unidentified snails	0.003	0.1	0.00
Total Gastropoda	6.4	326.1	1.00
Porifera			
<i>Spongilla</i> sp.	0.03	1	0.03
Osteichthyes			
unidentified fish	0.01	3	0.08
Other			
lead shot	0.03	1	0.03
Grand Total	113	3721.1	100.00

67% of insect biomass. The shortface lanx or limpet (*Fisherola nuttalli*) and Columbia pebblesnails (*Fluminicola* sp.) accounted for 8% of the common goldeneye diet. Plant matter, mostly achenes of pondweeds (*Potamogeton* spp.), smart weed (*Polygonum* sp.) and *Scirpus* spp. accounted for 5% of the biomass. Crayfish (*Pacifastacus* sp.) and unidentified minnows were recorded in trace amounts.

Elsewhere on the Detroit River, Michigan, Jones and Drobney (1986) found that common goldeneyes fed largely on plant matter, mostly wild celery (*Vallisneria americana*). Oligochaetes, small crustaceans, and minnows were also consumed. On the Mississippi River, Thompson (1973) reported that gastropods and pelecypods were important foods of common goldeneyes in the fall.

Studies of common goldeneye diets in marine waters generally document a similar preference for invertebrates and mollusks. However, while aquatic insect larvae are consumed in freshwater, crustaceans are consumed in marine waters. Cottam (1939) pooled marine and freshwater diets of common goldeneye and reported that they fed mostly on animal matter (crustaceans, aquatic insects, and mollusks), with 26% of the food being plant material (mostly *Potamogeton*). Nilsson (1972) found that common goldeneye along the Swedish coast ate mainly mussels and polychaetes. Olney and Mills (1963) and Olney (1965) found that common goldeneye fed primarily on crustaceans and shore crabs (*Carcinus* sp.). Vermeer and Levings (1977) reported that in Boundary Bay, British Columbia, the common goldeneye fed mostly on crustaceans, crabs (*Cancer* sp., *Telmessus* sp.), shrimp (*Upogebia*), and amphipods. Madsen (1954) found that crustaceans (shrimp, *Crangon* sp., prawns, *Palaemonetes*), and isopods, and to a lesser extent bivalves and gastropods (periwinkles, *Littorina* sp.) were consumed by common goldeneye in Denmark. In Puget Sound Washington, Hirsch (1980) reported that common goldeneye foraged predominantly on crustaceans, along with small amounts of fish and gastropods. Dominant prey items were shore crabs (*Hemigrapsus nudus*), crabs and shrimp (*Heptacarpus* sp.); *Lacuna unifasciata*, a small snail, was the dominant gastropod and blennies (*Apodichthys flavidus*) were also taken.

Barrow's goldeneye diets were generally similar to those of common goldeneye (Table 2). Aquatic trichopteran larvae accounted for 82% of

the biomass; limpets (lanx) and snails accounted for 17%. However, Barrow's goldeneye diets contained less plant matter than did the diets of common goldeneye; only 1% consisted of *Potamogeton* and *Scirpus* achenes. Crayfish and unidentified minnows were recorded in trace amounts.

No other dietary studies have been reported for Barrow's goldeneye since 1939. Cottam (1939) reported on foods eaten by 71 adults, mostly from British Columbia, during 11 months of the year. Insects (odonata naiads, trichoptera larvae, midge larvae) constituted 36% of the diet by volume; mollusks (*Mytilus*) 19%, crustaceans (amphipods, isopods, crayfish) 18%, other animal foods 4%, and plant materials (*Potamogeton* and *Vallisneria*) 22%. Munro (1939), using some of Cottam's analysis, and additional samples, reported on the contents of 116 stomachs. Salmon eggs, mollusks, crustaceans, and marine algae were eaten by coastal-inhabiting birds. Inland-dwelling birds ate insects, mostly trichoptera larvae, odonata naiads, crustaceans (amphipods, crayfish) and plant materials.

In our studies, both goldeneye species fed on pebblesnails and shortface lanx. The distribution and abundance of these mollusk species are poorly known (Neitzel and Frest 1993). Columbia pebblesnail (*F. columbiana*) and shortface lanx are "Candidate Species" for potential listing as threatened or endangered by the U.S. Fish and Wildlife Service, and the State of Washington has placed them in their Special Animal Species list (WDG 1983). Considering the biomass of lanx and snails consumed by goldeneyes, both mollusk species must have occurred commonly enough to provide an important food source for these birds.

Weights

Weights of common and Barrow's goldeneyes (adults and subadults) are shown in Table 3. Nelson and Martin (1953) reported that weights of male common goldeneyes averaged 997 g, with a maximum of 1,406 g. Weights of female common goldeneyes averaged 815 g with a 1,133-g maximum. Subadult weights were not reported. Nelson and Martin (1953) also reported weights of Barrow's goldeneye: males averaged 1,087 g with a maximum of 1,314 g, while females averaged 725 g with a maximum of 861 g. Johnsgard (1975) reported an average weight for male Barrow's goldeneye at 1,162 g with a maximum of

TABLE 2. Food items in Barrow's goldeneye collected on the Yakima and Columbia rivers, 1955-1957

Taxa	Average Weight Per Bird	Total Wet Weight (g)	% Total
Plant Matter			
unidentified vegetation	0.3	10.0	0.18
<i>Potamogeton pectinatus</i> achenes	0.4	14.0	0.25
<i>Polygonum hydropiper</i> achenes	0.1	4.0	0.07
<i>P. lapathifolium</i> achenes	0.4	14.0	0.25
<i>Scirpus acutus</i> achenes	0.1	3.0	0.05
Total Plant Matter	1.3	45.0	1.00
Animal Matter			
Insecta			
unidentified larvae	1.1	41.0	1.00
Coleoptera adults	0.1	2.0	0.04
Corixidae adults	0.1	2.0	0.04
Odonata naids	0.1	2.0	0.04
<i>Brachycentrus</i> sp. larvae	86.5	3374.0	61.00
<i>Hydropsyche cocherelli</i> larvae	26.1	1019.0	18.00
<i>Cheumatopsyche campyla</i> larvae	1.8	70.0	1.00
unidentified ephemeroptera naids	0.1	5.0	0.09
Total Insecta	116.9	4515.0	82.00
Gastropoda			
<i>Fisherola nuttalli</i>	19.0	756.0	14.00
<i>Fluminicola columbiana</i>	4.5	177.0	3.00
<i>Gyraulus</i> sp.	0.003	0.1	0.00
<i>Stagnicola apicina</i>	0.4	15.0	0.37
unidentified snails	0.03	1.0	0.02
Total Gastropoda	23.93	949.1	17.00
Porifera			
<i>Spongilla</i> sp.	0.03	1.0	0.02
Osteichthyes			
unidentified fish	0.06	0.2	0.00
Grand Total	142.22	5510.3	100.00

TABLE 3. Weights (g) of adult and subadult common and Barrow's goldeneyes from Southcentral Washington

Age/Sex	common goldeneye			Barrow's goldeneye		
	Range	Mean $\pm$ SE	N	Range	Mean $\pm$ SE	N
Adult						
Male	776-1246	1060.2 $\pm$ 33.36	14	980-1315	1130.5 $\pm$ 18.69	18
Female	505-833	720.2 $\pm$ 88.00	5	577-857	750.7 $\pm$ 24.33	10
Subadult						
Male	875-1025	986.0 $\pm$ 30.52	6	832-1113	977.8 $\pm$ 67.53	4
Female	397-736	599.3 $\pm$ 39.86	8	609-818	736.0 $\pm$ 44.73	5

SE = standard error, N = number of samples

1,219 g, while females ranged from 793.8 to 907.2 g. Yocom (1970) reported weights of Barrow's goldeneye collected in August; males averaged 1,020.6 g, while females averaged 595.4 g. These data were obtained when goldeneyes weighed the least because they were molting and females were still recovering from nesting and rearing young (Yocom 1970). Weights reported in our study are generally comparable to those reported by others. However, adult and subadult weights (Table 3) demonstrated age-related differences that should be considered in bioenergetic analyses. Body-weight dynamics may reflect resource availability and competition, which in turn may influence winter distribution, migration and habitat use by sexes.

Conclusions

This paper summarizes eight years of data on the winter diet and body-weight dynamics of Barrow's and common goldeneyes in a freshwater environment in the Pacific Northwest. Weights reported in our study were similar to those reported by others. On the Columbia and Yakima rivers, common and Barrow's goldeneye diets were generally

similar and included large numbers of insects and mollusks. Common goldeneye ate more plant matter than Barrow's goldeneye. Mollusks were more important in the diet of Barrow's goldeneye. Few other data are available for Barrow's goldeneye. Comparison with other studies of common goldeneye show that while aquatic insect larvae are consumed in freshwater environs, crustaceans are consumed in marine habitats.

Acknowledgments

One June 3, 1992, Richard E. Fitzner was killed in an airplane crash while conducting wildlife surveys. He had studied bird and other wildlife populations in the mid-Columbia Basin for two decades. He will be sorely missed. We thank the many hunters who provided samples of goldeneye digestive systems. Jerry Davis was involved in collecting the specimens. We also thank Charles A. Brandt, Lisa E. Fitzner, Robert L. Newell, and William A. Radke for helpful suggestions in the preparation of this manuscript. This work was supported by the U.S. Department of Energy under Contract DE-AC06-76RLO 1830 with Battelle Memorial Institute.

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Summer and Autumn Temporal Activity of the Montane Vole (*Microtus montanus*) in the Field

Abstract

Because little is known of the temporal activity of the montane vole (*Microtus montanus*) under natural conditions, this field study was undertaken to elucidate the summer and autumn activity patterns. Laboratory studies suggest this species is more nocturnal when subject to long photoperiods that simulate summer conditions. The temporal activity of the montane vole was continuously monitored 3-5 days/week May-November, over two successive years, in an old-field grassland in southeastern Washington. Live traps, instrumented with timer mechanisms that documented capture times, were checked twice daily. Voles were active at all hours of the day and night but both sexes and all age groups were predominately diurnal. In June, September, October, and November, 1989, the diurnal activity was significantly greater than expected ($p < 0.05$). A diurnally bimodal activity pattern was apparent during the summer months. Activity was reduced during the highest daytime temperatures. It is suggested that photoperiod, ambient temperatures, energetic requirements, predatory pressures, and interspecific competition may influence the temporal activity pattern.

Introduction

Temporal activity patterns are an important aspect of better understanding the ecological niche of a species, however, little had been published about the temporal activity of the montane vole (*Microtus montanus*) when Madison (1985) extensively reviewed the literature on activity rhythms of *Microtus*. The few published studies he cited were all conducted in the laboratory (Seed and Khalili 1971, Baumgardner *et al.* 1980, Dewsbury 1980, Rowsemitt 1981, Rowsemitt *et al.* 1982). While laboratory investigations on the activity rhythms of the montane vole have continued (Rowsemitt and Berger 1983, Rowsemitt 1986, 1989, 1991), only Claypool (1984) has reported on the temporal activity in the field for this species.

Numerous field studies on activity rhythms have been conducted on *Microtus* species other than the montane vole. Madison (1985) concluded in his review that the activity schedule through the diel period of most species is flexible and that the free-running rhythms during constant light or darkness (Calhoun 1945, Seed and Khalili 1971, Lehmann 1976, Daan and Slopeema 1978) supported the existence of circadian rhythms. Field studies on voles often find diurnal or crepuscular activity, whereas voles under laboratory conditions (including *M. montanus*) are reportedly nocturnal (Calhoun 1945, Heidt 1971, Seed and Khalili 1971, Herman 1977, Rowsemitt *et al.* 1982, Claypool 1982, 1984).

Rowsemitt *et al.* (1982) demonstrated in the laboratory that a change in photoperiod can induce male *M. montanus* to shift its locomotor activity

from a nocturnal to a diurnal pattern. Rowsemitt (1991) recently compared those results with running wheel activity of female *M. montanus* and observed nocturnal activity under long photoperiods to be less likely in females than in males.

Field studies have also shown some *Microtus* species emphasize diurnal activity during the winter and then shift to crepuscular or nocturnal activity in the summer (Baumler 1975, Carley *et al.* 1970, Erkinaro 1961, Lehmann 1976). Ambrose (1973) reported a tendency for *M. pennsylvanicus* to be diurnal during the summer in natural environment enclosures.

Differences in the temporal activity of age and gender of some microtine species have been reported by several investigators (Pearson 1960, Evans 1970, Baumler 1975, Lehmann and Sommersberg 1980). This study investigates the temporal activity of the montane vole in the field during summer and autumn to elucidate the patterns of activity with respect to gender and ages, and to determine if this species is more nocturnal than diurnal in the summer.

Materials and Methods

Study Area

The 2.6 ha study area is in an old-field grassland surrounded by wheat fields immediately west of Robison Pond (300 m), 5.6 km n.w. of Walla Walla, (n.e. quarter, section 7, T7N, R36E), Walla Walla Co., WA. The site is dominated by teasel (*Dipsacus sylvestris*) and a variety of grasses (*Agropyron* sp., *Bromus* spp., *Festuca* sp., *Poa* spp.,

and *Polypogon* sp.). Fuel reduction burning in the area is practiced every few years, and most recently in November, 1989.

Data Collection

Data were collected over 13 months in May-July, and September-November, 1989, and May-November, 1990. Sherman live traps (six in 1989 and 18 in 1990), instrumented with timing mechanisms, were spaced 5 m, baited with oats and carrots (during summer months) and left open continuously for two, three (June, 1990) or five (June and July, 1989, and July and August, 1990) consecutive days each week. The traps were checked and baited twice each day. Captured voles were sexed, weighed, aged (adults > 33 g; subadults 22-33 g; juveniles < 22 g), ear-tagged with Monel no. 1 tags (National Band and Tag Co., Newport, KY), and released. The timing mechanisms on the traps are a modification of a field timer described by Jenness and Ward (1985) and are powered with 4-rechargeable AA batteries. The timers are activated with a magnet switch when the trap door shuts. Elapsed time is read from eight light emitting diodes (LED) recording 5, 10, 20, 40, 80, 160, 320, and 640 minutes respectively, to accumulate 1275 min (= 21 hrs 15 min) from the time the trap door shuts. Any combination of LED's could be recorded, and the total elapsed time indicated, subtracted from the time of recording, documented the capture time within a 5 min accuracy. Traps were covered with a 2500 cm² vinyl tarp for protection against the elements. Ambient temperature and relative humidity were continuously recorded with a hygrothermograph (Model 5020, Qualimetrics Inc., Sacramento, CA). Mean ambient temperatures were determined for every even hour, all days of the month, for each month. For May, July, and September, 1989, temperature-humidity data were recorded for only 17, 19, and 15 days respectively.

Data Analysis

A capture index was developed to reflect the trapping success each month. The index was based on the total number of voles captured, divided by the total number of trap-nights and trap-days X 100. An analysis of the 495 capture times showed only 6.4% (32) to represent crepuscular activity, thus the 12 (2.4%) captures during morning twilight were pooled with diurnal captures and the 20

(4.0%) captures during evening twilight were included with the nocturnal captures. The sunrise and sunset times for each month were averaged to calculate the percent of lightness during the 24 hr. The monthly capture frequencies (%) for each even hour of the 24 hr day were determined by using the nearest hour of capture.

I tested the null hypothesis that no difference existed in the observed occurrence of voles between day and night. I took changing daylength into account and calculated the expected values from the true proportions of daylength over the sampling period. For example, in June it was light on the average 65% of the 24 hr day. The χ^2 test was used to test the differences between the expected number of diurnal occurrences and the observed number of diurnal occurrences and differences were considered statistically significant at the 0.05 level.

Results

A total of 482 individual *Microtus* were trapped 495 times. Based on weight, there were 97 juveniles, 215 subadults, and 170 adults. Individuals were seldom recaptured, and in 11 of 13 months, 80-95% of the captures were one time captured individuals. The greatest number of voles were caught during July and August, 1990, and the fewest in October and November, 1989, while the greatest trapping success was May-July, 1989 (Figure 1).

The percent difference between the percent of light in the 24 hr day, taking changing daylength

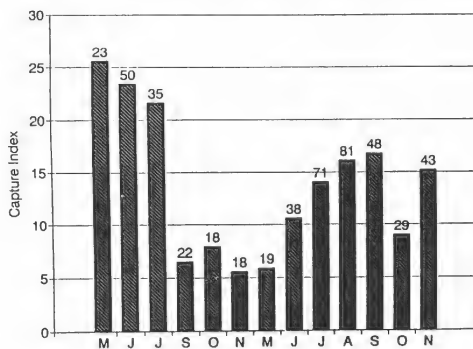


Figure 1. Capture indices, based on the total number of voles captured divided by the total number of trap-nights and trap-days X 100, reflect the trapping success for each month. Numbers above each bar represent the total voles captured.

into account, and the percent of diurnal vole activity observed is shown for each month in Figure 2. Vole activity was never more nocturnal than expected. In 1989 diurnal activity was significantly greater than expected in June ($\chi^2 = 10.63$, $p < 0.001$), September ($\chi^2 = 8.54$, $p < 0.001$), October ($p < 0.05$), and November ($p < 0.05$). In July, 1989, the vole activity was strongly diurnal ($\chi^2 = 3.23$, $p < 0.1$). There was a strong difference between the percent of diurnal activity in 1989 and 1990.

A bimodal diurnal activity pattern appeared during July through October, both years (Figs. 3 and 4). The greatest activity period occurred most frequently during the 3 hr period before sunset and subsequent to peak ambient temperatures. In November, 1990, the activity was greatest (25.5%) during the 3 hr period before midnight; in September, 1990, it was greatest during the 3 hr period following sunrise. The period of least activity in 11 of the 13 months was between midnight and sunrise. In September, 1990, between 1000 and 1600 hrs, there was 9% less activity than between midnight and sunrise. Between 0800 and 1400 hrs in October, 1990, there was 46% less activity than between midnight and sunrise. In seven of the 13 months, no voles were captured at the 2200, 2300, or 2400 hr, and in nine of the 13 months none were captured during the 0200 hr.

The sex ratio of captured males to females averaged 1:1.1. There was no significant difference at the $P < 0.05$ level of the male:female captures during any month. Throughout the 13 month trapping period, the vagrant shrew (*Sorex vagrans*), the deer mouse (*Peromyscus maniculatus*), the western harvest mouse (*Reithrodontomys megalotis*), and the house mouse (*Mus musculus*) were other species periodically captured.

Discussion

The obvious diurnal summer activity, and other temporal patterns found in this study, are similar to patterns described by Claypool (1984) in the only field study on temporal activity previously reported for this species. He described monthly activity patterns over a two year period of a population of montane voles near the southwest edge of the Great Salt Lake in Utah. The voles at his field site, at 41° N, experienced a photoperiod pattern (summer solstice is 15 h 09 min) similar to

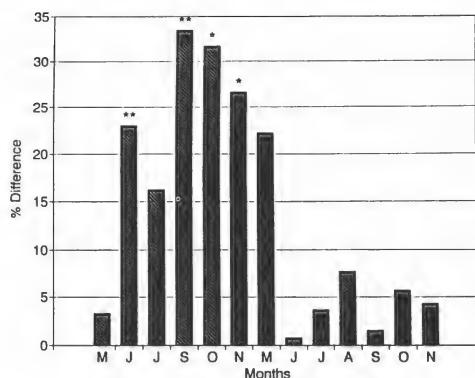


Figure 2. The percent of differences between the percent of light in the 24 hr day, taking changing daylength into account, and the percent of diurnal vole activity observed each month. Significant differences: *, $P < 0.05$; **, $P < 0.001$.

the photoperiod at this 46° N site (summer solstice is 15 h 45 min). He described vole activity as predominately diurnally bimodal in the summer and activity at all hours in the summer and fall. He reported late afternoon activity peaks in October and November, and a decrease of activity during the hottest period of the day.

There was no difference in activity patterns of males and females seen in this study. Claypool (1984) did not collect field data on gender difference for *M. montanus*. Rowsemitt (1991) recently reported a major difference in the temporal distribution of laboratory running wheel use by female *M. montanus* under long (16 h light : 8 h dark) and short (8 h light : 16 h dark) photoperiods, than what she and her colleagues had previously found for males (Rowsemitt *et al.* 1982). She found that females were less likely than males to be nocturnal under a long photoperiod. She feels that laboratory running wheel use, under long photoperiods, increases nocturnality to a greater degree than would be found under natural conditions. *M. pennsylvanicus* females have been found to be more diurnal than males by some (Evans 1970, Madison 1985), but other studies of this same species reported no difference in gender activity (Madison 1985). Pearson's (1960) study of *M. californicus* and Baumler's (1975) investigation of *M. agrestis* found no difference in activity patterns of males and females.

A bimodal activity pattern during the day was also reported for the montane ovle by Vaughan

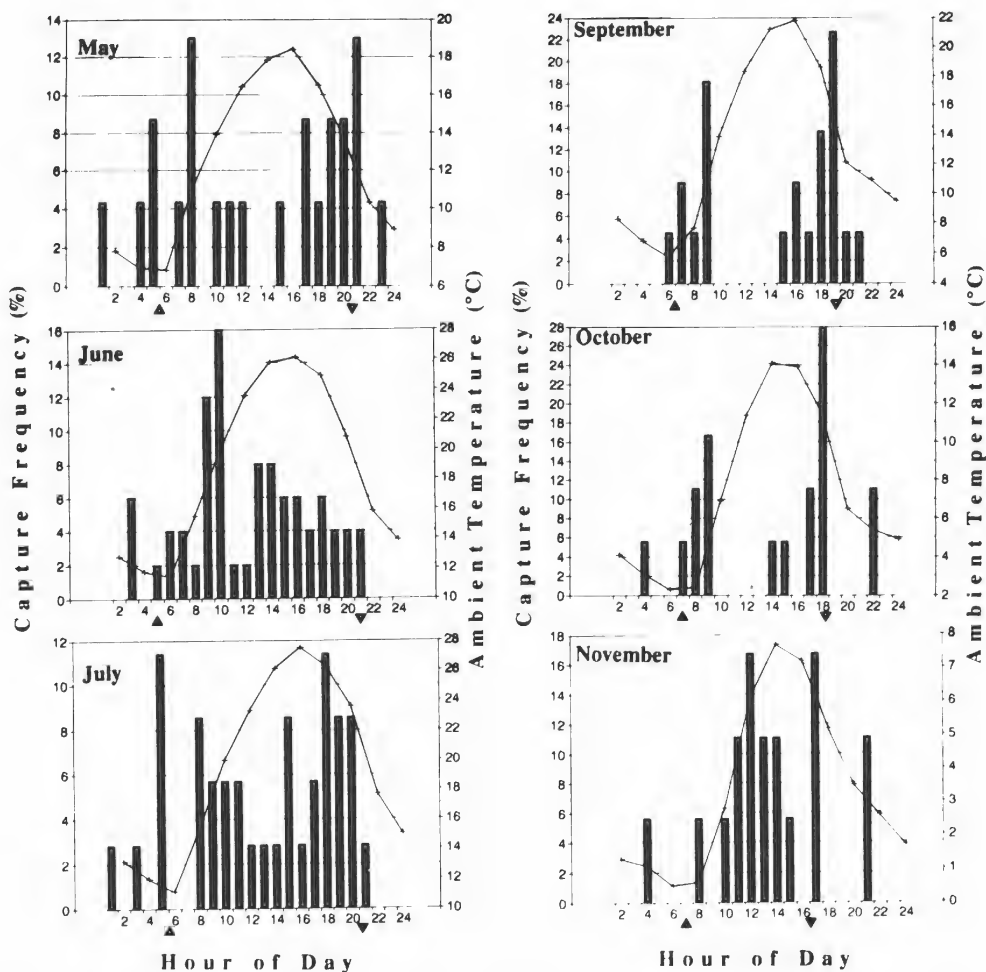


Figure 3. Capture frequencies and mean ambient temperature line through the hours of the day for each month of 1989. Upward and downward arrows at hours of day indicate the mid-month time of sunrise and sunset.

(1974). The highest summer temperatures in this study were typically 25-30°C and occurred from 1400-1800 hr. Packard (1968) reported that montane voles could not withstand temperatures much above 31°C. High daytime temperatures reportedly depressed the daytime activity in *M. californicus* (Pearson 1960) and *M. pennsylvanicus* (Getz 1961).

The activity at all of the day and night hours reported here probably reflects the energetic

requirements of the montane vole. Vaughan (1974) found the stomach contents of *M. montanus* to be entirely forbs and grasses. A low-quality herbivorous diet requires *Microtus* spp. to feed frequently throughout the 24 hr day (Daan and Aschoff 1981). Kenagy and Vleck (1982) found a relatively uniform metabolic level between day and night for *M. longicaudus* and *M. townsendii*.

The preponderance of the subadults (45%) and adults (35%) in the captured population in this

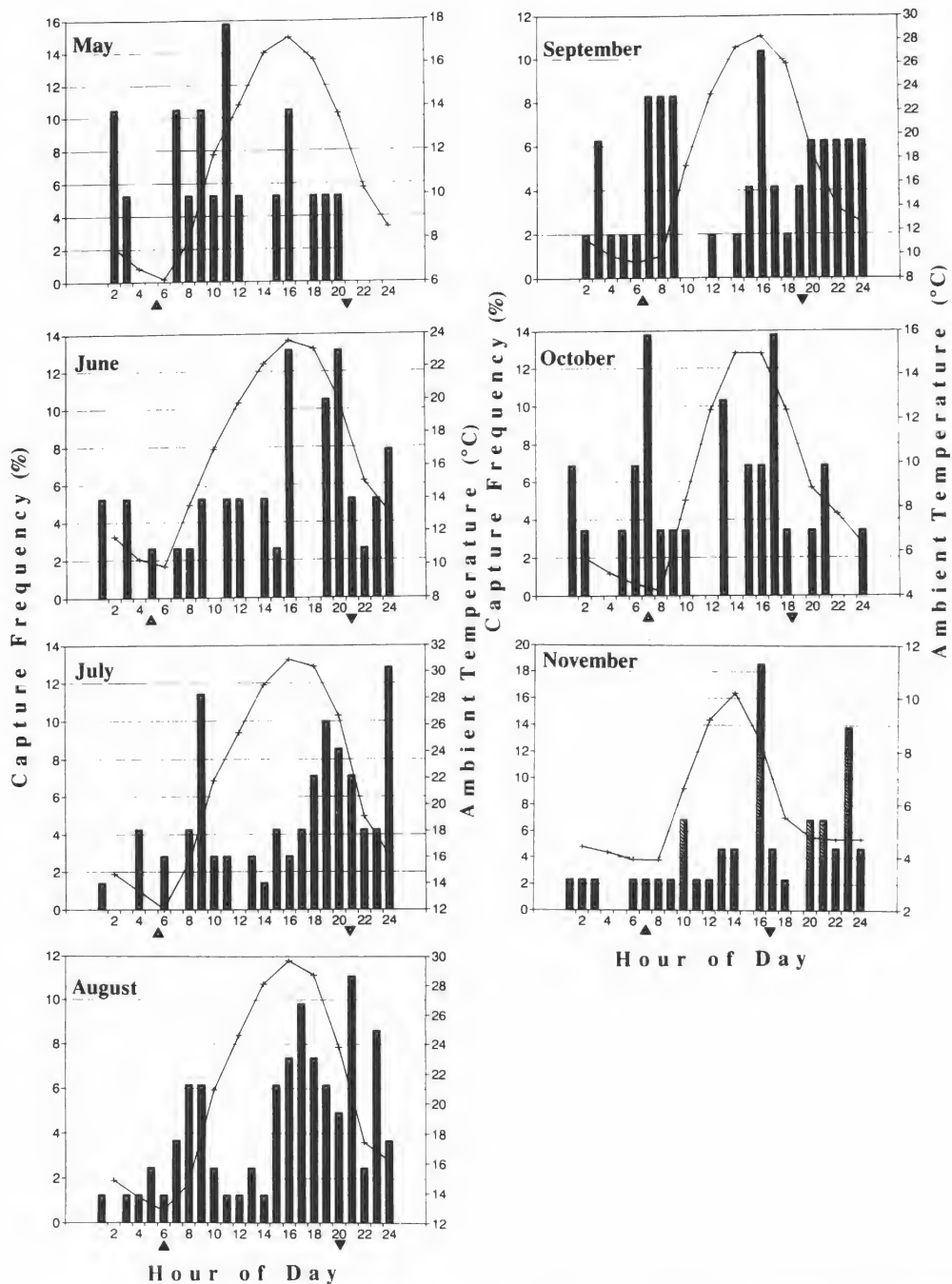


Figure 4. Capture frequencies and mean ambient temperature line through the hours of the day for each month of 1990. Upward and downward arrows at hours of day indicate the mid-month time of sunrise and sunset.

study may account for the diurnal activity pattern seen in the population as a whole. Nocturnal captures of juveniles equalled or exceeded diurnal captures during four months. The distribution of adult activity did not differ from that of the juvenile *M. montanus* reported by Claypool (1984). Juvenile *M. arvalis* and *M. agrestis*, however, were found to be more nocturnal than adults by Hoogenboom *et al.* (1984) and Baumler (1975). Baumler suggested the juveniles might avoid the daytime competition presented by the adults.

Parasitism, predation, and competition are three kinds of interspecific interactions that Madison (1985) suggested correlated with temporal activity in microtines. Parasites have been shown to change the rhythmic behavior of *M. montanus* (Seed and Khalili 1971).

Predatory pressures might induce a predominately diurnal or nocturnal pattern in prey species such as microtines. Hamilton (1937) interpreted the crepuscular peaks of activity in *M. pennsylvanicus* as a strategy to avoid both nocturnal and diurnal predators. The diurnal activity of *M. pennsylvanicus*, in areas where the predatory short-tailed shrew, *Blarina brevicauda*, occurred, was suggested as predation avoidance by Fulk (1972). Another survival strategy of prey species could be to synchronize activity periods with others in the population for exposure to predators in order to benefit from safety in numbers. The activity pattern of a population of *M. arvalis*, preyed on by kestrels, was hypothesized to reflect this strategy (Daan and Slopeema 1978, Rijnsdorp *et al.* 1981), although Lehmann and Sommersberg (1980) interpret the synchronous locomotor behavior of *M. arvalis* differently. They feel it is more important for intraspecific communication while defending a family territory.

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The activity of the vole population in this study was more strongly diurnal in 1989 than in 1990. Hawks and kestrels are often observed in this study site. Perhaps there was a difference in the population densities of both voles and diurnal aerial predators (e.g. hawks) between 1989 and 1990. This might have influenced the vole activity and accounted for the significantly greater number of diurnal occurrences by voles.

Finally, interspecific competition for space with other small mammals might have influenced the temporal activity of this vole population. *Sorex vagrans*, *Peromyscus maniculatus*, *Reithrodontomys megalotis*, and *Mus musculus* are known to be present in the study site. Interspecific use of shared runways could be accomplished by temporal avoidance. This behavior was interpreted in the interactions of cotton rats and prairie voles by Glass and Slade (1980). Carley *et al.* (1970) found in their field study, peaks of diurnal activity of *Microtus ochrogaster* to be exclusive from the peaks of nocturnal activity of *P. maniculatus* and *R. megalotis*.

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Randy G. Hein, Eastmont Animal Clinic Inc., P.S., 100 Valley Mall Parkway, East Wenatchee, Washington 98802

Patricia A. Talcott, Department of Food Science and Toxicology, Holm Research Center, University of Idaho, Moscow, Idaho 83843

Jack L. Smith, Washington Department of Wildlife, 48-B Devonshire Road, Montesano, Washington 98563

and

Woody L. Myers, Washington Department of Wildlife, N. 8702 Division Street, Spokane, Washington 99218

Blood Selenium Values of Selected Wildlife Populations in Washington

Abstract

The object of this study was to determine blood selenium (Se) values in free ranging wild ungulates in Washington state. Blood was obtained from elk (*Cervus elaphus nelsoni*, *C. elaphus roosevelti*) in the Blue, Cascade, and Olympic Mountain Ranges, the Department of Energy's Hanford Site and the Yakama Indian Nation Reservation; California bighorn sheep (*Ovis canadensis californiana*) from the north Cascade Range and northeastern Washington, and moose (*Alces alces shirasi*) from the Mt. Spokane area were sampled. Mule deer (*Odocoileus hemionus hemionus*) from the north shore of Lake Chelan were also sampled. When compared to adequate livestock standard values (Se > 0.1 ppm, wet/weight) Blue Mountain elk, Yakama Indian Nation Reservation elk, bighorn sheep, and mule deer were marginally deficient (Se 0.05-0.09 ppm) whereas the moose sampled were deficient (Se < 0.05 ppm). Elk located on the Olympic Peninsula and Hanford Site exhibited Se values considered adequate. The results suggest blood Se levels vary among elk herds within the state while bighorn sheep, mule deer, and moose have generally low Se values when compared to domestic livestock with adequate values.

Introduction

Selenium is a trace element that is an integral part of the enzyme, glutathione peroxidase, which acts in conjunction with vitamin E to protect cellular membranes and lipid containing organelles from the destructive effect of fatty acid peroxidation (Blood and Radostits, 1989, The Merck Veterinary Manual, 1991). The primary clinical deficiency disease occurring in domestic ruminants is nutritional muscular dystrophy, commonly called white muscle disease. In affected animals this malady is most significant in young animals during rapid growth. Signs include stiff gait, reluctance or inability to stand and muscle tremors if forced to stand more than a few minutes. Weakened myocardium and diaphragm muscle results in tachycardia and labored abdominal respiration. Death is not an unusual sequela. Other Se deficiency conditions include unthriftiness, chronic diarrhea, decreased growth rate, poor hair coat, impaired immune response, and possibly decreased reproduction (Blood and Radostits, 1989). Domestic cattle blood Se values are considered adequate when > 0.1 ppm, marginal when between 0.05-0.09 ppm, and deficient when < 0.05 ppm (Fielder, 1986).

Normal blood Se levels in nondomestic ruminants are not well known. In red deer, post

capture myopathy is predisposed by Se deficiency and white muscle disease was diagnosed in trapped mountain goats in southeastern British Columbia (Herbet *et al.*, 1971). Farmed red deer exhibiting unthriftiness responded to injectable Se (Knox *et al.*, 1987, Mackintosh *et al.*, 1989). However, captive white-tail deer which were fed a Se deficient diet did not exhibit adverse health effects (Brady *et al.*, 1978).

Soils of the Pacific Northwest are generally low in Se (Blood and Radostits, 1989) and Se deficiency in livestock in the region has been long recognized (Muth and Allaway, 1963). Compared to livestock standards, Se deficiency has been reported in black tail deer herds in California (Flueck, 1991), wild mountain goats in Washington (Robbins *et al.*, 1985, Fielder 1986), and mule deer and Rocky Mountain elk in Washington (Fielder, 1986). Captive mountain goats exhibited normal comparative Se values when fed enriched (0.1 ppm selenium) feed (Robbins *et al.*, 1985).

In California from 1980 through 1988, 1,695 mule deer blood samples were analyzed for Se content (Oliver *et al.*, 1990). In that statewide survey of 15 management groups, mean values ranged from 0.039 mg/L (ppm) to 0.178 mg/L with the overall mean 0.089 mg/L and the authors report

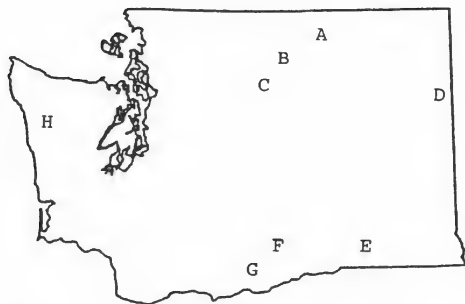


Figure 1. Wildlife populations sampled in Washington. A Vulcan Mountain bighorn sheep, B Sinlahekin Wildlife area bighorn sheep, C Lake Chelan mule deer, D Mt. Spokane moose, E Blue Mountains elk, F Hanford Site elk, G Yakama Indian Nation elk, H Olympic Mountains elk

widespread deficiency based on low first quartile values in two-thirds of the management groups and deficient values (<0.04 ppm Se) in all sample groups. Between 1980 and 1989, 1 Roosevelt and 7 tule elk herds were tested for blood selenium levels in six California counties. Mean Se values of twenty animals from each herd varied from 0.075 ppm to 0.258 ppm (Jessup, 1990). Only one herd exhibited a mean Se value <0.1 ppm.

The object of this study was to determine blood Se values in free ranging wild ungulates from various regions of Washington.

Materials and Methods

Description of Study Areas

Individual capture areas are identified in Figure 1. Twenty Roosevelt elk were captured on the southern and western drainages of the Olympic Mountains (OM) outside Olympic National Park. The elk were found in timber clear cuts with elevation generally between 370-1077 meters. Sixty-four Rocky Mountain elk were captured in the Blue Mountains (BM) of southeastern Washington. The elk were located in mountain meadows, timber clear cuts, and shrubsteppe range with elevation varying between 300-1540 meters. Twenty Rocky Mountain elk were captured at the Hanford Site (HS) in southcentral Washington. The animals inhabit shrubsteppe range with elevation ranging between 275-465 meters. Fourteen Rocky Mountain

elk were captured on the Yakama Indian Nation Reservation (YINR) in southcentral Washington. Elevation at the capture sites ranged from 460 to 1385 meters and habitat varied from thin coniferous forest to shrubsteppe. Four California bighorn sheep were captured on the Sinlahekin Wildlife Area (SWA) on the northeastern slopes of the north Cascade Mountains, and 10 from Vulcan Mountain (VM) in northeastern Washington. Elevation at these capture sites was approximately 615 meters. The bighorn sheep were captured on steep hillsides with cliffs and thin timber stands. Two moose were captured on the southern and southeastern slopes of Mt. Spokane (MS) in replanted young growth clearcuts. Elevation at the capture sites ranged from 850 to 1000 meters. Six mule deer were sampled along the north shore of Lake Chelan (LC) at elevations of 340-430 meters on steep, south facing slopes. Vegetation was dominated by Douglas fir, Ponderosa pine, bluebunch wheat grass, and bitterbrush.

Capture Methods

Two moose were darted from a helicopter using Palmer Cap-Chur[®] darts containing 1.8 mg carfentanil (Wildnil[®]) and 50 mg xylazine (Rompun[®]) in January 1992. Carfentanil was reversed with 200 mg naloxone; one-third given intravenously with the remainder administered subcutaneously. Adult elk and calves over 9 months old were captured in the BM by darting with immobilizing drugs from a helicopter in March of 1990 and 1991. These elk were darted with 1.8-3.6 mg carfentanil and 50-100 mg xylazine. Carfentanil reversal was achieved with 200-250 mg naloxone administered as noted previously. Renarcotization of the elk was not observed during follow up radiotelemetry flights. In June 1992, 13 neonate calves (<1 month old) were captured in the BM by net gunning from a helicopter or physical restraint of calves found hiding in thick cover. In March 1992, 20 Roosevelt elk were captured in the OM by darting from a helicopter with concentrated xylazine (300 mg/ml). Total dosages ranged from 900 to 1,800 mg/elk. Drug reversal was accomplished by intravenous injection of 40-60 mg yohimbine (Yobine[®])/elk. In March 1992, at the SWA, one bighorn sheep was captured by helicopter darting with a combination of 600 mg ketamine/120 mg xylazine and three were captured in a drive net.

Reversal was with yohimbine. In March of 1992, 7 Rocky Mountain elk on the YINR and 4 on the HS were captured by helicopter darting using a combination of carfentanil (2.1-4.2 mg/elk) and xylazine (50-100 mg/elk). Carfentanil was reversed with naloxone. In March 1993, 7 elk were captured on the YINR and 16 elk were collected at the HS. The elk were darted from a helicopter using carfentanil (2.5-8.0 mg/elk). This drug was reversed with naltrexone (250-800 mg/elk); one-fourth administered intravenously and the remainder subcutaneously. In March 1993, 10 bighorn sheep were caught by drive net at VM and 6 mule deer were sacrificed along the north shore of Lake Chelan.

In all animals except the mule deer, jugular venipuncture was used to collect blood samples which were immediately injected into EDTA blood tubes. Mule deer blood was collected by cardiocentesis. Blood samples were kept cool in the field and stored at 4°C prior to shipment. All samples were submitted for analysis within 7 days of capture. Whole blood selenium was analyzed by inductively coupled plasma (ICP) spectrophotometer atomic emission using hydride generation (Tracy and Moller, 1990) at the Holm Research Center, University of Idaho, Moscow, and values were reported on a wet weight basis.

Results and Discussion

This survey of selected wildlife in Washington supports a previous study (Fielder, 1986) demonstrat-

ing low comparative selenium values in deer, mountain goats and elk. One-hundred forty wild ungulates were sampled for blood Se values. These animals included 2 moose, 118 elk, 14 bighorn sheep, and 6 mule deer (Table 1). Selenium values ranged from 0.00 ppm to 0.49 ppm with a mean value of 0.085 ± 0.06 for all samples. Individual population mean values ranged from 0.015 to 0.12 ppm. The lowest mean value was noted from two moose near MS while the highest average mean value was found in elk located at the HS.

Although only two adult moose were sampled, their extremely low results would suggest deficiency. Both animals were in excellent physical condition. An adult cow was pregnant (determined by rectal palpation) and accompanied by a yearling when captured. The two California bighorn sheep populations sampled had Se values suggestive of marginal blood Se levels. Low Se values in SWA forage may be a factor resulting in poor lamb recruitment (R. Johnson, personal communication). Elk populations exhibited varied Se values. Elk captured in the OM exhibited significantly higher ($P < 0.05$) Se values than BM elk. Of interest is comparison of the OM elk and Olympic National Park mountain goat mean Se values. Robbins *et al.*, (1985) found 19 mountain goats, captured in 1983 and 1984, had a mean blood Se value of 0.041 ppm q 0.032 whereas the 20 elk in this study had respective values of 0.158 ppm q 0.108. Difference in these values may be related to time of year when sampled and elevation of home range.

TABLE 1. Blood Selenium values of wildlife in Washington.

Species	Location	Sample Size	Month/Year Sampled	Mean	Range	S.D.
Moose	Mt. Spokane	2	January 1992	0.015	0.01-0.02	
Elk (1)	Blue Mountains	13	June 1992	0.042	0.02-0.07	± 0.014
Elk (2)	Blue Mountains	51	March 1990 and 1991	0.061	0.00-.017	± 0.03
Elk (3)	Yakama Indian Nation	14	March 1992 and 1993	0.069	0.03-0.16	± 0.036
Elk (3)	Olympic Mountains	20	March 1992	0.158	0.01-0.49	± 0.108
Elk (3)	Hanford Site	20	March 1992 and March 1993	0.12	0.08-0.16	± 0.021
Bighorn Sheep	Vulcan Mountain	10	March 1993	0.079	0.04-0.13	± 0.033
Bighorn Sheep	Sinlahekin Wildlife Area	4	March 1992	0.097	0.07-0.13	± 0.027
Mule Deer	Lake Chelan	6	March 1993	0.081	0.058-0.15	± 0.03

(1) Calves less than one month old

(2) Calves nine months or older and adults

(3) Yearlings and adults

Elk captured at the HS displayed values significantly higher ($P < 0.05$) than BM elk. Neonate elk captured in the BM in June 1992 exhibited Se levels lower than adults captured in the same area in March 1990 and 1991. Mule deer from the north shore of LC had Se values similar to bighorn sheep values from the SWA and VM. Topography, local flora, and climate are similar among the areas although the sheep were captured at higher elevations.

In this survey several wildlife populations exhibited mean values considered deficient by livestock standards and two had values thought to be adequate. The majority (6) of the populations exhibited mean values suggestive of marginal blood Se levels. The significance of the marginal and de-

ficient values has not been established in wildlife populations in Washington. Reproduction, growth rate and recruitment are areas of interest for future management study.

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Feeding Ecology of Larval Fishes in Lake Roosevelt, Washington

Abstract

Food habits, feeding selectivity, and diet overlap were analyzed for larval walleye (*Stizostedion vitreum*), yellow perch (*Perca flavescens*), sculpins (*Cottus spp.*), and suckers (*Catostomus spp.*) collected in Lake Roosevelt, Washington, in May to July 1982. Larval diet of fishes in this unique co-occurring species mix has not been previously described. Larval fishes 4-25 mm long were sampled weekly with 0.5-m townets from nearshore sites at two stations. Zooplankton was collected with Miller samplers to characterize food availability. The most abundant food items were calanoid copepods in walleye stomachs, calanoid and cyclopoid copepods in yellow perch stomachs, and cyclopoid copepods in sculpin stomachs. Larval walleyes 9 to 24 mm long also preyed upon larval fishes. Cladocerans were important food only to larval suckers, which fed almost exclusively on *Bosmina* and *Chydorus*. Feeding selectivity, determined by Wilcoxon's nonparametric signed-rank analysis, showed positive selection for several prey items among the fish taxa. Schoener's niche overlap values indicated significant diet overlap between walleye and yellow perch. During our study period, effects of competition on growth, survival, and character divergence of larval walleye and yellow perch was minor. Annual variation in reservoir conditions could result in stronger or weaker competitive interactions than we observed since zooplankton composition is known to influence fry feeding success and growth.

Introduction

The transition of larval fish from endogenous to exogenous feeders results in a "critical period" (Bagenal 1978) when availability of suitable prey has important effects on survival. The initial strength and ultimate success of percid year classes are usually determined during the first year of life, therefore the description of factors that can affect year class characteristics is important in the management of percid fisheries (Maloney and Johnson 1957; Forney 1976, 1980; MacLean and Magnuson 1977; Serns 1987). Although diet of coexisting larval walleye and yellow perch has been described for other areas (Maloney and Johnson 1957, Smith and Pycha 1960, Bulkley *et al.* 1976, Keast 1979), it has not been reported from the Columbia River system, which supports the largescale (*Catostomus macrocheilus*) and bridgelip (*C. columbianus*) suckers and the prickly sculpin (*Cottus asper*) which are not found elsewhere in the range of these percids.

We documented food habits of coexisting larval walleye, yellow perch, sculpins, and suckers in Lake Roosevelt. Zooplankton consumption by larval fishes was compared to abundance of zooplankton in the water, and prey selectivity was evaluated. We considered diet overlap in conjunction with prey availability and selection data to de-

scribe potential competitive interaction in the larval fish assemblage.

We expected diets of larval percids in Lake Roosevelt would be dissimilar to those reported from other systems, with the difference attributable to regional prey availability and potential competitive interactions resulting from diet overlap with unique co-occurring species.

Study Area

Lake Roosevelt, the largest lake in Washington, includes that portion of the Columbia River and its tributaries impounded by Grand Coulee Dam (Figure 1). The reservoir is 243 km long, has a surface area of 33,490 ha, a maximum depth of 122 m, and a maximum width of 3.4 km. Stober *et al.* (1980) provided a detailed account of the limnology, geography, and climate of the lake and surrounding area.

Walleye and yellow perch, believed to have been introduced into the Columbia River system in the late 1940s (Bregé 1981), were first reported in Lake Roosevelt in the early 1960s (Fletcher 1987). The walleye has become an important sport fish in the lake, adding 1.5 to 2.5 million dollars annually to the local economy (Beckman *et al.* 1985). Porcupine Bay, located in the Spokane River arm of the reservoir, is reported to have the highest sport fishery harvest rates of walleye in Washington (Fletcher 1987). This economic significance, the popularity and success of angling for walleye, and a lack of fishery-related information

¹Current address: U.S. Forest Service, Payette National Forest, Krassel Ranger District, P.O. Box 1026, McCall, ID 83638

²To whom correspondence should be addressed

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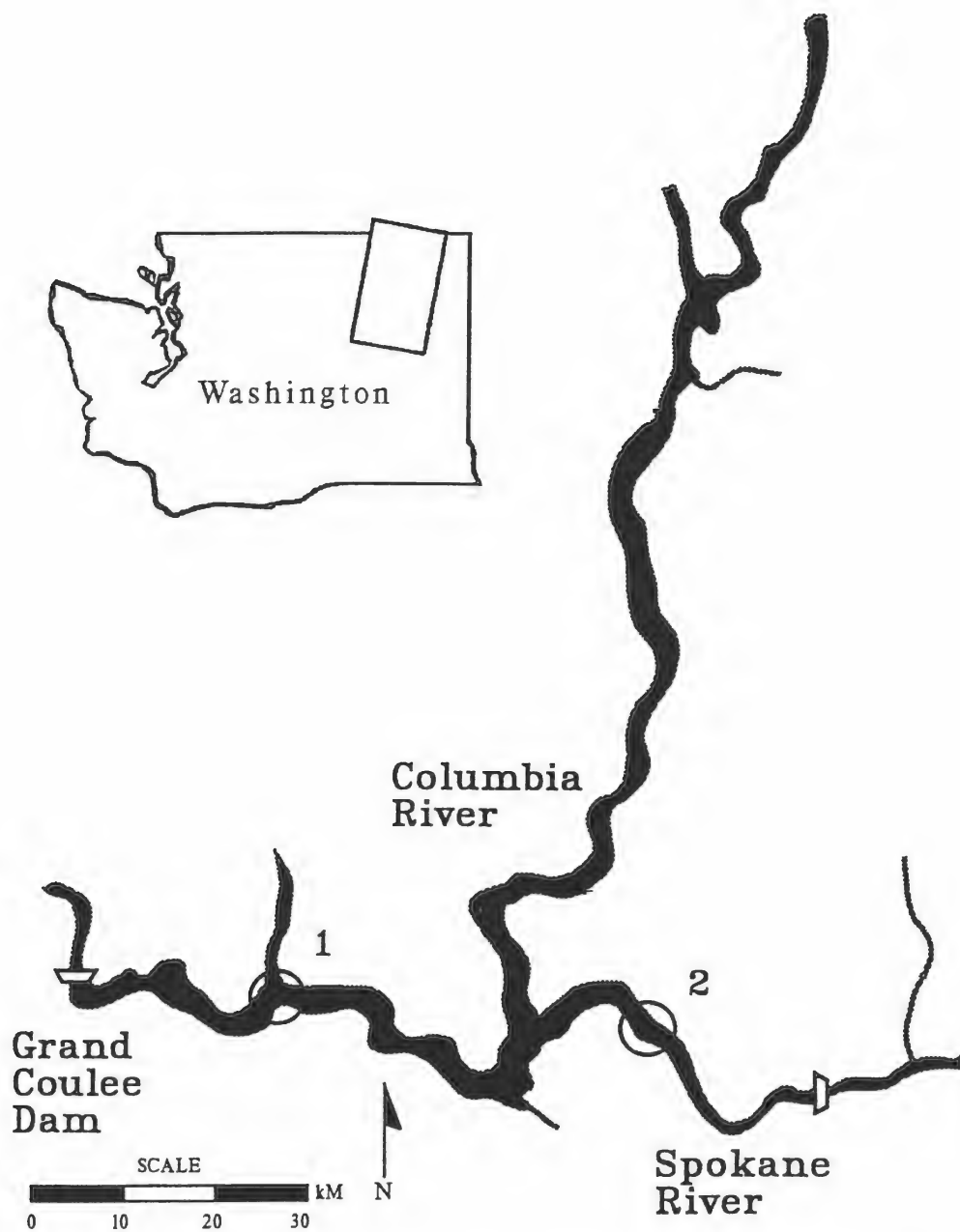


Figure 1. Location of sampling stations 1 (mouth of Sanpoil River) and 2 (Porcupine Bay), Lake Roosevelt, Washington.

regarding Lake Roosevelt prompted a fisheries and limnology investigation by the U.S. Fish and Wildlife Service (Beckman *et al.* 1985), of which the present study was a part.

Methods

Sampling was conducted at two stations in the lower reservoir: station 1, located at the mouth of the Sanpoil River, and station 2, within Porcupine Bay of the Spokane River arm (Figure 1). An embayment site and a tributary confluence site were sampled at each station.

We sampled larval fish and zooplankton weekly from 26 May to 7 July, 1982 during daylight hours. Larval fish were collected with 0.5-m plankton nets of 760-micrometer mesh. Zooplankton were collected with high-speed Miller samplers fitted with 153-micrometer nets. A 1.8-m outrigger extending from the inshore side of the bow of the boat was used to tow the nets just below the water surface, as close as possible to shore at each sampling site. The actual water depth of the sampled area was between 0.5 m and 2.0 m, and usually the nets sampled from the top, middle, and bottom of the water column simultaneously. In standard sampling procedure, a 10-minute tow for larval fish was followed by a 2-minute tow for zooplankton. Samples were washed into collection jars and preserved in 10% formalin.

Zooplankton samples were diluted or concentrated to a known volume and then subsampled with a large-bore pipette (3 to 5 subsamples). Zooplankters were enumerated from the subsamples by use of a plankton counting wheel on a dissecting microscope. We used mean number of organisms of a given taxon from the subsamples to estimate the density (number/m³) and percent composition by number for each station and date.

Zooplankters were classified to suborder (copepods), developmental stage (nauplii), or genus (Cladocera). Because morphological characteristics of larval largescale, bridgelip, and longnose (*Catostomus catostomus*) suckers were too similar to allow specific identification, they were combined in the analyses. For the same reason, prickly, mottled (*Cottus bairdi*), and torrent (*C. rhotheus*) sculpins were combined.

Stomach contents from a random subsample of at least 10 larvae of each taxon (walleye, yellow perch, sculpins, and suckers) were analyzed from each tow (if available). Total length of each fish was measured, and ingested organisms were iden-

tified to the lowest practical taxon and enumerated. Percent composition by number was determined for each prey taxon. Stomach contents data from embayment and confluence sites were pooled by date and station to provide sufficient sample sizes for analysis, assuming no differences between sites. Because fish size is not an independent variable of time, analyses of food preferences based on fish size were not performed. We assumed that analyses of preferences over time reflected changes in fish size.

A two-sided Wilcoxon's signed-rank analysis was used to test selectivity of larval fish for major prey taxa (Kohler and Ney 1982), with a null hypothesis of no difference in relative prey abundance between stomachs and zooplankton samples. Statistical significance was assumed at the $p < 0.05$ level.

We calculated diet overlaps among the four fish groups at each station, using the niche overlap index (d_{xy}) of Schoener (1970). Percentages used were the numerical percent composition of each major prey taxon (calanoid and cyclopoid copepods, copepod nauplii, *Bosmina* spp., *Daphnia* spp., *Leptodora kindtii*, *Ceriodaphnia* spp., and *Chydorus* spp.) in pooled stomachs of fish of a given taxon. Niche overlap values range from 0 (no overlap) to 1 (complete overlap); values above 0.60 are generally considered to indicate biologically important overlap (Zaret and Rand 1971, Wallace 1981), but not necessarily competition.

Results

Zooplankton

Dominant zooplankton taxa included daphnids, *Bosmina* spp., and cyclopoid (*Cyclops* spp.) and calanoid (*Diaptomus* spp.) copepods. Overall, mean zooplankton densities were much higher at station 1 (12,408/m³) than at station 2 (2,353/m³), with the exception of *Bosmina* spp., which was approximately 10 times as abundant at station 2 (52,900/m³ compared to 5,973/m³) toward the end of the sampling period.

Food Habits

Walleye: Major food items in the stomachs of the 80 larval walleye examined were calanoid and cyclopoid copepods (Table 1). Larval fish and the cladocerans *Leptodora kindtii*, *Daphnia* spp., and *Diaphanosoma* spp. contributed minor percentages to the walleye diet.

TABLE 1. Number of examined stomachs (n), range of total fish lengths (TL), and percent composition (by number) of major prey items in nonempty stomachs of larval fish in Lake Roosevelt, Washington, 1982.

	Walleye ¹	Yellow Perch ²	Sculpins	Suckers ³
STATION 1				
n	27	257	43	0
Range TL (mm)	8-24	5-25	6-11	
Calanoid	66	55	12	
Cyclopoid	21	23	73	
<i>Bosmina</i> spp.	0	0	0	
<i>Daphnia</i> spp.	3	12	15	
Other	9	11	0	
STATION 2				
n	53	92	65	143
Range TL (mm)	9-22	4-17	4-9	9-24
Calanoid	58	5	24	0
Cyclopoid	0	75	70	5
<i>Bosmina</i> spp.	2	11	0	49
<i>Daphnia</i> spp.	5	5	6	1
Other	35	4	0	45

¹Other prey taxa included primarily larval fish and *Leptodora kindtii*.

²Other prey taxa included primarily *Ceriodaphnia* spp. and *Leptodora kindtii*.

³Other prey taxa included primarily *Chydorus* spp.

Only walleye preyed on other larval fish. Stomachs containing larval fish seldom contained other food items. One of the smallest walleye (9mm) contained larval fish that were 3 to 6 mm long. Walleye, yellow perch, sculpins, and suckers were among the fish species eaten. The percentage of larval fish in walleye diets was up to seven times higher at station 2 than at station 1.

Temporal changes in percent composition of individual prey items in walleye stomachs were evident, as exploitation of calanoid and cyclopoid copepods generally followed fluctuations in abundance of those populations in the sampling areas (Figure 2). The low level of predation on cyclopoid copepods at station 2 was an exception in view of the high abundance of that prey in the water column.

Yellow Perch: Calanoid and cyclopoid copepods and *Daphnia* spp. were the principal food items in the 349 larval yellow perch stomachs examined; others included *Bosmina* spp., *Ceriodaphnia* spp., and *Leptodora kindtii* (Table 1). Calanoid cope-

pods were dominant prey in stomachs of yellow perch at station 1, and cyclopoid copepods were dominant at station 2.

Both abundance and consumption of *Daphnia* spp. peaked late in the sampling period. Percent composition of copepods in stomach samples also approximated seasonal changes in the density of copepods in the reservoir (Figure 2).

Sculpins: Of 108 larval sculpin stomachs examined, 40% were empty. Most of these were from station 2, where only half of the stomachs contained prey. Cyclopoid copepods were the most numerous prey, followed by calanoid copepods and *Daphnia* spp. (Table 1). Sculpin lengths were small (compared to other fish taxa analyzed), ranging from 4 to 11 mm.

Suckers: Of the 143 suckers examined (all from station 2), 85 contained prey in their stomachs. Most empty stomachs were from fish 10 to 12 mm long, which still had yolk sacs. *Bosmina* spp., *Chydorus* spp., and cyclopoid copepods were the most numerous food items (Table 1). Suckers were the only fish sampled that preyed extensively on *Bosmina* spp. or *Chydorus* spp. The use of cyclopoid copepods was highest early in the sample period and steadily declined towards the end (Figure 2). A temporal increase in the use of *Bosmina* spp. accompanied an increase in its availability in the water column (Figure 2). Percent composition of *Chydorus* spp. in sucker stomachs ranged from 2 to 9% in early June to 47 to 67% in late June, dropping to 23% during the final week of sampling. *Chydorus* spp. was rarely collected in zooplankton samples at anytime (Wunderlich 1985).

Selectivity and Diet Overlap

Selectivity values for eight prey items were averaged for each fish taxon across stations and dates (Table 2). Larval walleye exhibited positive selection only for calanoid copepods, while larval yellow perch exhibited selection for *Daphnia* spp., *Ceriodaphnia* spp., and calanoid and cyclopoid copepods. Sculpins preferred cyclopoid copepods, while suckers preferred *Bosmina* spp., *Chydorus* spp., and cyclopoid copepods. Yellow perch was the only species that preferred *Daphnia* spp., and only suckers preferred *Chydorus* spp.

The Schoener niche overlap value between walleye and yellow perch was significant ($d_{xy}=0.84$) at station 1. All other overlap values were below 0.35 except for those between yellow

TABLE 2. Larval fish selectivity values and probability values (p) from Wilcoxon's signed-rank comparison tests for eight prey items, Lake Roosevelt, Washington, 1982. + denotes positive selection, - denotes negative selection, and R denotes random selection.

Prey	Walleye (p)	Yellow perch (p)	Sculpins (p)	Suckers (p)
Copepods				
Calanoid	+(0.00)	+(0.00)	R(0.06)	R(0.05)
Cyclopoid	R(0.21)	+(0.00)	+(0.01)	+(0.00)
Nauplii	-(0.00)	-(0.00)	-(0.00)	-(0.00)
Cladocerans				
<i>Bosmina</i> spp.	-(0.00)	R(0.69)	-(0.00)	+(0.02)
<i>Daphnia</i> spp.	R(0.75)	+(0.00)	R(0.69)	R(0.24)
<i>Chydorus</i> spp.	-(0.00)	-(0.00)	-(0.00)	+(0.00)
<i>Ceriodaphnia</i> spp.	-(0.03)	+(0.01)	-(0.00)	R(0.11)
<i>Leptodora kindtii</i>	-(0.06)	-(0.00)	-(0.00)	-(0.00)

perch and sculpin, which were 0.50 at station 1 and 0.57 at station 2.

Discussion

The relatively greater densities of zooplankton at station 1 could have been a result of warmer water at the embayment site (temperature was measured in a concurrent study, as reported by Beckman *et al.* [1985]). Zooplankton abundance and epilimnetic temperature have been reported to be strongly correlated (Walburg 1972, Patalas and Salki 1984).

The significance of larval fish and *Leptodora kindtii* to larval walleye may have been underestimated due to the size differences between these food items (which were 3 to 10mm long) and other ingested zooplankters (which were 0.5-2.0mm long). This size difference suggests a greater contribution by fish and *Leptodora kindtii* to the walleye diet in terms of energy biomass than the numeric analyses indicate. Although walleye have generally been found to begin consuming larval fish at lengths between 30 and 62 mm (Forney 1966, Walker and Applegate 1976, Mathias and Li 1982), we found larval fish in the stomachs of walleye as small as 9mm. This discrepancy could have been due to patterns in prey availability, as similarly concluded by Mathias and Li (1982), and indicated by differences in prey availability between stations 1 and 2. Stomachs of walleye from sta-

tion 2 contained appreciably more larval fish than did those from station 1. Though abundance of larval fish (as prey) at station 2 was not markedly different from that at station 1 (Wunderlich 1985), calanoid copepods, the generally preferred prey of walleye overall, were much less abundant at station 2. Low densities of this preferred food item may have influenced walleye to begin feeding on larval fish at an earlier age than if calanoid copepods had been more abundant.

Larval walleye were selective for calanoid copepods, the largest zooplankters consistently encountered in Lake Roosevelt, even when other prey items were more abundant. The larger mouth gapes and better-developed teeth in larval walleye relative to larval yellow perch, sculpins, or suckers enable walleye to ingest larger prey (Mathias and Li 1982). Similar size selectivity has been documented for walleye elsewhere. Larval walleye in Oneida Lake, New York, were selective for cyclopoid copepods, which were larger than the co-occurring calanoid copepods in that system (Houde 1967). Walker and Applegate (1976) found positive selection for calanoid copepods, the largest prey available, in young-of-the-year walleye in South Dakota, while Mathias and Li (1982), in field and laboratory studies in Manitoba, observed a positive size selectivity for cyclopoid copepods.

Calanoid and cyclopoid copepods were major items in the diet of larval yellow perch in Lake Roosevelt. Yellow perch fed more heavily on copepods than on *Daphnia* spp., though selectivity values were positive for both. Yellow perch larvae depended on copepods in northern Minnesota (Siefert 1972), Iowa (Bulkley *et al.* 1976), and before they reached 30 to 35 mm in Oneida Lake, New York (Mills *et al.* 1984), but ate *Daphnia* spp. almost exclusively in Manitoba (Wong and Ward 1972) and in Oneida Lake after reaching 30 to 35 mm (Hansen and Wahl 1981, Mills *et al.* 1984). These dissimilarities may be explained by variation in geographical and temporal prey abundance. In the present study, utilization of *Daphnia* spp. was highest when they were at peak abundance in the water column.

Sculpins rapidly become benthic during early life stages (Sheldon 1968, Wallus and Granneman 1978), which would explain the patchy distribution (Wunderlich 1985) and small size of the sculpins we collected. Cyclopoid (76.4%) and calanoid copepods (8.3%) and *Daphnia* (15.3%) were the most important food items at station 1. The high

incidence of empty stomachs, similarly reported by Bailey (1952) for larval sculpins, indicated that exogenous feeding had not yet begun in many sculpins that were vulnerable to the collection gear. By the time complete exogenous feeding had begun, sculpins were probably able to avoid the townets or had become benthic.

Larval suckers ate *Bosmina* spp. and *Chydorus* spp., the smallest mature zooplankters sampled in Lake Roosevelt, almost exclusively. Mouth size of young-of-the-year suckers has been shown to limit food intake to small prey items (Stewart 1926, MacPhee 1960). Consumption of small cladocerans (as well as other prey) by larval suckers was reported from Idaho (MacPhee 1960) and from Shuswap Lake, British Columbia (Carl 1936). However, MacPhee (1960) did not find the degree of feeding specialization that we observed in Lake Roosevelt and labeled the feeding of larval suckers as "indiscriminate." Dependence of suckers on *Bosmina* spp., numerically the most abundant zooplankter at station 2, suggested that suckers in Lake Roosevelt were highly opportunistic, rather than indiscriminate feeders.

Because the bottom-dwelling *Chydorus* spp. was probably not effectively sampled by our towed nets, its use by fish was consistently greater than its apparent availability. Use of *Chydorus* spp. was expected to increase as suckers increased in size and adopted benthic feeding modes, as described by MacPhee (1960) and Stewart (1926), but no increase was seen in Lake Roosevelt. The influence of a highly abundant prey item (*Bosmina* spp.) appeared to have a greater effect on species selectivity than did the influence of changing feeding morphologies.

Overlap, defined as "the use, typically at the same time, by more than one organism of the same resource regardless of resource abundance," may indicate competition for a resource, which has been defined as "the demand, typically at the same time, of more than one organism for the same resource of the environment in excess of immediate supply" (Weatherly 1963, Zaret and Rand 1971). Diet overlap, then, could suggest competition for a shared prey resource only when that prey resource is in short supply (Hurlbert 1978, Abrams 1980).

Overlap values were high between walleye and yellow perch at station 1, with both species preying extensively on calanoid copepods. Though overall abundances of calanoid copepods were higher at station 1 than at station 2, there were seasonal periods of relatively low abundance. During those times, the use of calanoid copepods by both walleye and yellow perch was high (Figure 2). Overlap values and positive selection of calanoid copepods by both percids over a range of densities suggested that trophic competition between larvae of walleye and yellow perch in Lake Roosevelt was occurring. Our hypothesis that diets of larval percids in Lake Roosevelt would differ from those reported from other systems, due to unique co-occurring species, was rejected.

In a discussion of the controversy over interspecific competition, Schoener (1982) indicated that when competition occurs only seasonally during infrequent "lean" times, it is considered too weak to significantly influence character divergence or species exclusions. Because the indicated competition and the documented switch to alternate prey observed for walleye at station 2 was localized and of short duration, the potential effects of competition on growth, survival, and character divergence of walleye and yellow perch are considered minor in Lake Roosevelt. Since no between-year comparisons are available, the potential importance of competition is indicated only for the year studied. The importance of competition may be stronger or weaker than observed here, depending on conditions varying between years. In years when stronger competition occurs, it could have a larger effect on year-class strength, which is important to fishery managers.

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and

Sherry Barrett, U. S. Fish and Wildlife Service, 4600 Kietzke Lane, Building C, Reno, Nevada 89502-5093

Distribution of Amphibians and Reptiles Along the Truckee River System

Abstract

From 28 May to 22 August 1992, an intensive survey of the amphibians and reptiles along the entire length of the Truckee River system was conducted during drought conditions. The main objective was to determine the current distribution of amphibians and reptiles (especially obligate aquatic/riparian species) within this river system. Four amphibian and 8 reptilian species were observed. Of these 12 species, 5 (42%) are obligate aquatic/riparian species: the western toad (*Bufo boreas*), northern leopard frog (*Rana pipiens*), Pacific chorus frog (*Pseudacris regilla*), bullfrog (*R. catesbeiana*), and western aquatic garter snake (*Thamnophis couchi*). Only two species (Pacific chorus frog and western terrestrial garter snake (*T. elegans*)) were found along the entire Truckee River. The distribution of the northern leopard frog appears to be decreasing and is now restricted to only a small stretch of the river. The decreased distribution of the leopard frog in the Truckee is possibly due to success of the introduced bullfrog. No Great Basin spadefoot toads (*Spea intermontana*), mountain yellow-legged frogs (*R. muscosa*), or western pond turtles were observed. Based on the literature and our knowledge of the local herpetofauna, individuals of these species should occur within the Truckee River system. The results of this study that indicate declines in amphibian distribution and population size correlate with other investigations in the Northwest, other parts of the United States, and the world.

Introduction

The Truckee River originates in California at Lake Tahoe near Tahoe City and flows for about 161 km into the Great Basin where it empties into Pyramid Lake in northwestern Nevada. During normal conditions, the rate of flow is more than 14,004.5 l per second with most of the water coming from Lake Tahoe. The lake water flows over a natural rim at an elevation of 1,900 m. The Truckee River also gains water from its many tributaries as it flows toward Pyramid Lake, which is situated at an elevation of 1,198 m. Several tributaries have been dammed to counter water shortages. Thus, during drought conditions when the river carries about 2,839 l per second or less, much of the river's flow comes from these reservoirs.

Because the Truckee travels through such a range of elevations, the ecosystems associated with the river vary from forests (both evergreen and deciduous), mountain meadows, meadows, and marshes, to cold desert shrub. At the lower elevations, the Truckee River is often bordered by agricultural and urban developments.

The upper part (about 65 km) of the river from Lake Tahoe almost to Verdi flows primarily through evergreen forest that contains ponderosa pine (*Pinus ponderosa*), jeffrey pine (*P. jeffreyi*), and lodge-

pole pine (*P. contorta*) with a few marshy areas that have small ponds and a few mountain meadows. This upper stretch of the river has a fast to moderate rate of flow and would be classified as a mountain stream or river. The lower stretch of the Truckee from about Verdi to Pyramid (about 96 km) flows through a deciduous forest that contains primarily black cottonwood (*Populus trichocarpa*) and fremont cottonwood (*P. fremontii*), a few agricultural areas, a few marshy areas, some small municipalities, the cities of Reno and Sparks, and an extensive cold desert shrub area typical of the Great Basin. This lower stretch of the river has a moderate to slow rate of flow, typical of a large valley stream or river. Much of the lower stretch, especially that part of the river between Wadsworth and Pyramid Lake is slow and pondlike. Beaver and beaver dams are found along the entire river. The dams create pondlike areas and are more prevalent during drought conditions. During normal conditions, dams are broken due to the high rate of flow, especially in the upper parts of the river.

There is little information about amphibians and reptiles along the Truckee River. Linsdale (1940) and La Rivers (1942) reported on the amphibians and reptiles in Nevada, including specimens collected along the Truckee River. Banta

(1965) published a distributional checklist of amphibians and reptiles inhabiting the state of Nevada, which also contained some information on the herpetofauna found along the Truckee River. Finally, Stebbins (1966) and Behler, et al. (1979) wrote field guides that include some coverage of herpetofauna along the Truckee River.

The objective of this study was to determine the current distribution of amphibians and reptiles (especially obligate aquatic/riparian species) within the various ecosystems along the Truckee River system. Throughout the northwest, other regions of the United States, and the world, amphibian populations appear to be declining. Thus, another objective of this study was to examine for declines in amphibian populations in the Truckee system.

Methods

This study was conducted during drought conditions from 28 May to 22 August 1992. The study was an intensive ecological survey of the amphibians and reptiles along the entire length of the Truckee River System. In addition, we examined sites on the Little Truckee River between Stampede and Boca Reservoir. We measured environmental factors such as water temperature and Ph at each study site.

We selected a total of 31 study sites: 27 along the Truckee River, two along the Little Truckee River, and two at ponds located close to the Truckee River (Figure 1 and Table 1). We located study sites at an average distance of 6.1 km apart to ensure coverage of the entire Truckee River. We also selected study sites that were accessible and that appeared to have favorable habitat for amphibians and reptiles.

We investigated the study sites three times during 1992 (Table 2). The three census periods ensured that data would be collected on breeding and tadpole development. We examined a minimum of 0.4 km of river at each study site. During an investigation, binoculars were used to assist in identification. We used dip nets to collect amphibians, aquatic snakes, and potential prey such as small fish. Sample amphibian larvae were preserved in vials for later identification in the laboratory.

We recorded habitat characteristics for each amphibian or reptile that was observed, and, if the animal was on land, we recorded the distance from

the river. We also noted potential prey and predators in the area.

At the study site we recorded ambient temperatures, water temperatures, water Ph, rate of flow, and water depth. During the first census period, the ambient temperature was recorded at various times of the day. During the second and third census periods, the ambient temperature was recorded at the first site visited, midday, and at the last site visited. Water temperature was recorded at a depth of about 2.5 dm. The pH was recorded with an electronic pH meter. Rate of flow was classified as slow, moderate, or rapid. The water depth was measured when it remained constant throughout the study site and was estimated when it varied at a site.

Results and Discussion

Environmental Factors—Mean ambient temperatures for the three census periods were 26 (range 18-35°C), 24 (range 15-31°C), and 23°C (range 14-35°C), respectively. Thus, ambient temperatures were highly favorable for both amphibian and reptilian activity throughout all three census periods. Ambient temperatures were somewhat low for a relatively short period of time on only two days—on July 6, at 0910, the temperature was 15°C and on August 17, at 0920, it was 14°C. Also, on two days, ambient temperatures were fairly high for a short period of time—on June 4, at 1455, the temperature was 35°C and on August 17, at 1605, it was 35°C.

Average river temperatures for the first, second, and third census periods were 18 (range 13-27°C), 20 (range 14-29°C), and 21°C (range 17-28°C), respectively. Even though these recorded river temperatures were on the average lower than ambient temperatures, they were favorable for both amphibian and reptilian activity.

A general increase in river temperature from Lake Tahoe to Pyramid Lake was observed, with relatively low river temperatures from Lake Tahoe to about Reno 13 to 20°C; (Study Site 1 to 21), and relatively high temperatures from Lovelock to Pyramid Lake 20 to 28°C; (Study Sites 22 to 31). These temperature differences explain the distribution of some species along the Truckee. For example, bullfrogs (*Rana catesbeiana*) prefer pondlike environments or slow-moving streams with much aquatic and emerging vegetation associated

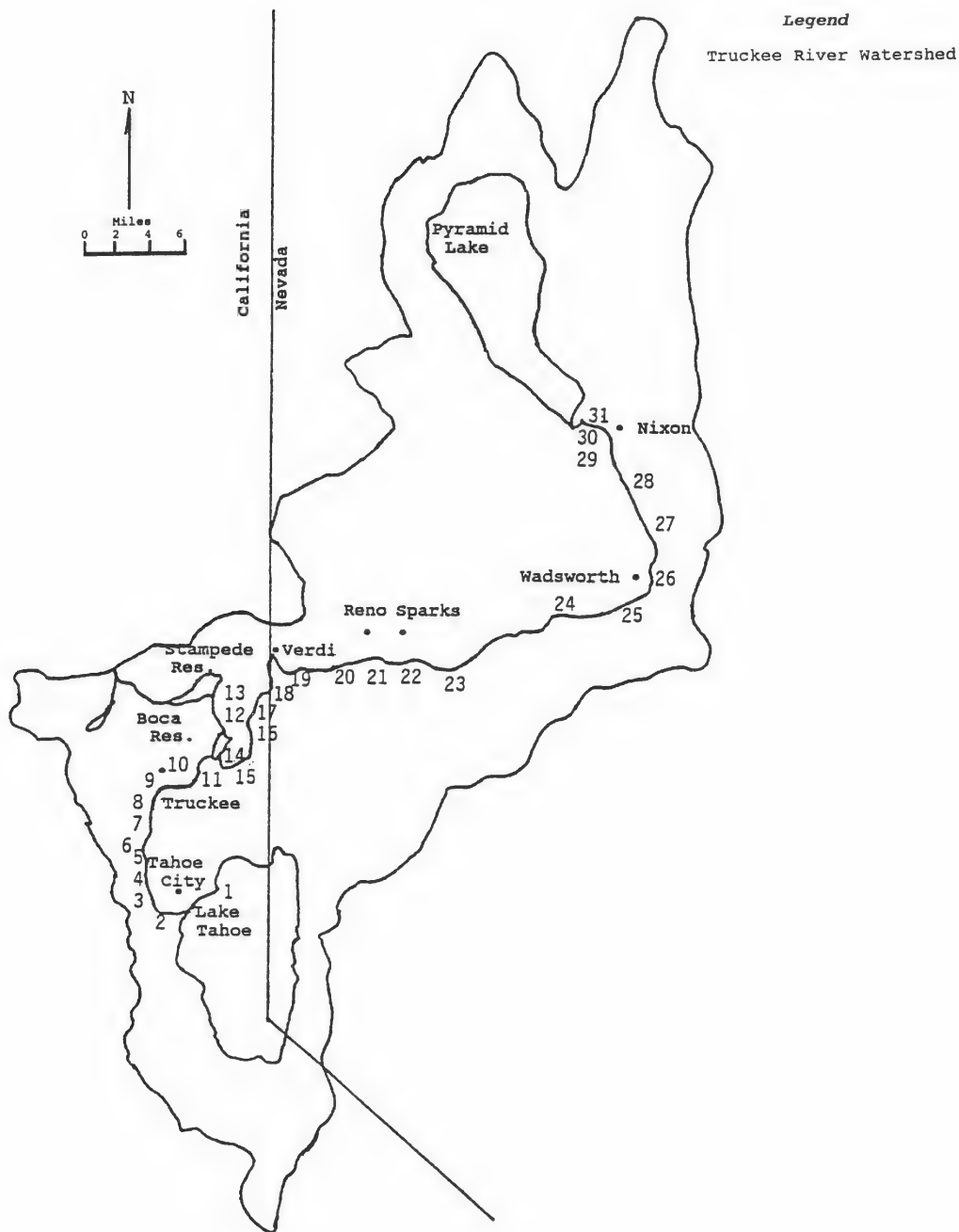


Figure 1. Map of the study area. The numbers indicate the approximate locations of the 31 study sites. The outer line depicts the Truckee River Watershed.

TABLE 1. Name and elevation of the 33 study sites.

Study Site	Elevation (m)	Study Site Name
1	1900	Lake Tahoe
2	1900	Fanny Bridge
3	1896	Twin Crags
4	1894	American Gas
5	1886	River Ranch Inn
6	1866	Squaw Creek
7	1826	Bullshead
8	1805	Cabin Creek
9	1791	Granite Flat
10	1759	Truckee
11	1709	Prosser
12 ¹	1731	Boca Rest Campground
13 ¹	1731	Boyington Mills Campsite
14	1677	Hirschdale
15	1659	Hirschdale Bridge
16	1616	Floriston
17	1580	Farad
18	1515	Coldron Ditch
19 ¹	1497	Verdi Pond
20	1416	Mayberry Park
21	1391	Oxbow Park (Reno)
22	1338	Lockwood
23	1306	Tracy Clark Power Plant
24A ¹	1288	Derby Dam Oxbow
24B	1288	Derby Dam (River)
25	1270	Orchard
26	1241	Wadsworth Bridge
27	1220	S bar S
28	1213	Dead Ox Wash
29	1208	Little Nixon
30	1201	Nixon Bridge
31	1198	North Nixon

¹These sites are not on the Truckee River. They are on streams that flow into it or they are ponds located close to the river.

with fairly high water temperatures. The distribution of bullfrogs in the Truckee River System only includes the lower, often pondlike, stretch of the Truckee. Bullfrogs were first encountered at the Coldron Ditch study site (Study Site 18).

Average pH of the Truckee River increased from 8.0 in early summer, to 8.2 in mid-summer, and to 8.9 in late summer.

Amphibians tolerated a pH range of 6.0 to 10.4. It does not appear that the pH of the Truckee River influenced the distribution patterns of the various amphibians.

TABLE 2. Days afield, time afield, and distance censused for each census period.

Days Afield	Numbered Field Days	Time Afield (Hrs.)	Distance Censused (Km)
5/26-6/12	5	21.00	20.2
7/6-7/13	4	17.50	21.8
8/14-8/22	3	12.75	18.1
Totals	12	51.25	60.1

The drop in elevation between Lake Tahoe and Reno is about 549 m, and only 152 m between Reno and Pyramid Lake, resulting in a faster rate of flow in the upper Truckee River. The slower rate of flow of the lower Truckee contributes to the pondlike habitat associated with this stretch of the river. These flow rates are important in explaining distribution of herpetofauna along this river system.

Although this study was conducted during drought conditions, during all three censuses the depth and amount of flow was sufficient to sustain a variety of fish and amphibian species. The biggest difference in flow occurred between the second and third censuses. At some of the sites during the third census (August 14 to August 22), there was a noticeable decrease in flow due to closure of Boca Reservoir. Only sites 19 (Verdi Pond) and 24A (Derby Dam Oxbow) were completely dry. At site 21 (Oxbow Park, Reno) a pond next to the river was completely dry during the second census (July 6 to July 13).

Throughout the study the level of Lake Tahoe was below the natural rim, and water was pumped from the lake over the rim. Water pumped from the lake generated some fairly large pondlike areas in the Truckee River immediately downstream from Lake Tahoe. The Truckee River accumulated additional flow from small tributaries.

Species of Amphibians and Reptiles Observed—During this study, we observed four amphibian species in three different families (Table 3). Of the four species observed, two are strictly aquatic forms—the bullfrog (*R. catesbeiana*) and the northern leopard frog (*R. pipiens*). In the adult stage, the Pacific chorus frog is semi-terrestrial. Also, the western toad (*B. boreas*) is essentially terrestrial in the adult stage.

Five lizard species in two families were observed along the Truckee River (Table 3). All five

TABLE 3. List of amphibian and reptilian species observed during this study.

Family	Scientific Name	Common Name
ORDER: Salientia or Anura (Frogs and Toads)		
Bufonidae	<i>Bufo boreas</i>	Western Toad
Hylidae	<i>Pseudacris regilla</i>	Pacific Chorus Frog
Ranidae	<i>Rana pipiens</i>	Northern Leopard Frog
	<i>Rana catesbeiana</i>	Bullfrog
ORDER: Squamata (Lizards and Snakes)		
Iguanidae	<i>Gambelia wislizenii</i>	Longnose Leopard Lizard
	<i>Sceloporus magister</i>	Desert Spiny Lizard
	<i>Sceloporus occidentalis</i>	Western Fence Lizard
	<i>Uta stansburiana</i>	Side-blotched Lizard
Teiidae	<i>Cnemidophorus tigris</i>	Western Whiptail
Colubridae	<i>Pituophis catenifer</i>	Gopher Snake
	<i>Thamnophis couchi</i> ¹	Western Aquatic Garter Snake
	<i>Thamnophis elegans</i> ²	Western Terrestrial Garter Snake

¹Subspecies: *T. e. couchi*; Sierra Garter Snake

²Subspecies: *T. e. elegans*; Mountain Garter Snake

species are well adapted to dry habitats and can be found away from free water. However, many individuals were often noted close to the river in riparian habitats. All of these lizards include insects in their diet, which are abundant in riparian habitats.

All three snake species observed during the study are in the family Colubridae (Table 3). Of these three species, the western aquatic garter snake (subspecies: Sierra Garter Snake (*Thamnophis couchi couchi*)) is primarily aquatic. The gopher snake (subspecies: Great Basin Gopher Snake (*Pituophis catenifer deserticola*)) and the western terrestrial garter snake (subspecies: Mountain Garter Snake (*Thamnophis elegans elegans*)) occur in both terrestrial and aquatic habitats.

Of the 12 amphibian and reptilian species observed during the study, only five species (42%) are obligate aquatic/riparian species: the western toad, Pacific chorus frog, northern leopard frog, bullfrog, and western aquatic garter snake.

Based on literature and our knowledge of the local herpetofauna, 20 species of amphibians and reptiles may occur on the Truckee River system. Of these 20 species, only three are obligate aquatic/riparian species: the Great Basin spadefoot toad (*Spea intermontana*), mountain yellow-legged frog (*R. muscosa*), and the western pond turtle (*Clemmys marmorata*).

The Great Basin spadefoot toad has been reported to be associated with the Truckee River

system (Linsdale, 1940; La Rivers 1942; and Banta, 1965). Preferred habitats for this species include rivers, ponds, springs, reservoirs/lake, irrigation overflows, sagebrush flats, and piñon-juniper woodlands (Fichter, et al., 1964; Stebbins, 1966). In the Truckee River system, most of the suitable habitat for this species is found in the lower elevations especially that part of the river close to Pyramid Lake, and individuals of this species have been collected at the southern end of the lake (Linsdale, 1940).

The mountain yellow-legged frog has been reported in the Lake Tahoe region (Linsdale, 1940 and Banta, 1965). Suitable habitat for this species is streams with moderate flow and rocky bottoms. This habitat is found in much of the upper Truckee River. However, it is unlikely that the mountain yellow-legged frog occurs in the main part of the river system because of the presence of trout. Bradford (1989) discovered that viable populations of mountain yellow-legged frogs cannot coexist with trout (*Salmo*) and brook trout (*Salvelinus*) which prey on tadpoles. It is possible that this frog is found in some tributaries to the Truckee River that have suitable habitat for this frog species and do not contain predatory fish species.

Toulouse (pers. comm.) reported three pond turtles (*C. marmorata*) at Oxbow Park in a 1.1 m deep pond, which contained many cattails. He also reported that one of the three turtles entered the Truckee River, which is connected to the pond

by a small stream. If the western pond turtle is still extant in the Truckee River, the population size is very small, and this species may be extremely vulnerable to eradication. This species was recently petitioned for listing under the Endangered Species Act (Jennings, et al., 1992; unpublished manuscript). Burroughs (pers. comm.) stated that in about June, 1993, members of the U.S. Fish and Wildlife Service decided that they would not list the western pond turtle as an endangered species. Their reason for not listing it was insufficient data, especially data that indicates a lack of substantial recruitment.

Distribution and Habitat of Amphibians Observed—

Three species of amphibians (the Pacific chorus frog, bullfrog, and western toad) were observed at more than one site, whereas the northern leopard frog was found at only one site along the Truckee River (Table 4). The Pacific chorus frog is the only amphibian species that appears to be located along the entire Truckee River. The bullfrog is distributed throughout the lower Truckee from the Coldron Ditch downstream to Pyramid Lake. The distribution of the western toad along the Truckee appears to be limited to a few areas along the lower Truckee River. However, numbers of tadpoles (thousands at site 30) and later toadlets at these sites were very high, suggesting a fairly large population of adult toads.

It appears that the distribution of the northern leopard frog along the Truckee has been restricted to only a small stretch of the river at study site 28. Linsdale (1940) reported northern leopard frogs

on the Truckee River at Verdi and at 15.3 km east of Reno. At study site 28, northern leopard frogs were found in both the river and in a spring-fed pond about 80 m to the east of the river. The pond was about 100 m long, 14 cm deep, with a muddy bottom. Much of the pond was surrounded by bulrush (*Scirpus acutus*). A stretch of about 10 m of the northeastern edge of the pond consisted of salt grass and sedges (0.3 m high) growing in a wet substrate. We observed several northern leopard frogs in this area. The edges of the river at this site have grasses, clover (*Trifolium*), sedges, and rushes. During the first census, four of the five adults were found around the northeastern edge of the pond, and one was noted along the river. During the second and third censuses, more frogs were observed along the river (31 frogs) than along the edges of the pond (2 frogs). It appears that the frogs moved from the pond to the river sometime between the first and second census. It's possible that in late spring or early summer, the frogs moved to the pond to breed, and then moved back to the river. The presence of either eggs or larvae in the pond would have confirmed this pattern; however, no eggs or larvae were noted in the pond throughout the study.

The lower Truckee from about Lockwood downstream has ample breeding and adult habitat for a variety of amphibian species. This section of the river is generally pondlike with a slow rate of flow; shallow, warm water; and large quantities of aquatic vegetation including *Elodea*, *Spirogyra*, and duckweed (*Lemna*) that offer excellent cover for tadpoles, froglets, and toadlets. Also, emerging vegetation (especially bulrushes, sedges, and a variety of grasses) along the edges of the lower Truckee River offer excellent cover. In contrast, the upper Truckee River, from Lake Tahoe downstream to about Verdi is lacking in breeding habitat, i.e., breeding ponds for egg and larval development. During drought conditions, major side channels of the river become excellent breeding ponds that contain adequate aquatic and emerging vegetation. During this study we observed Pacific chorus frog larvae in such habitats. It is possible that during normal conditions, this observed reproduction does not occur.

*Distribution and Habitat of Reptiles Observed—*We observed most of the lizards along the lower Truckee River from site 23 (Tracy Clark Power Plant) downstream to Pyramid Lake (Table 9),

TABLE 4. Specific localities along the Truckee River where amphibian and reptilian species were found.

Species	Study Sites
<i>Bufo boreas</i>	22, 30, 31
<i>Pseudacris regilla</i>	4, 6, 15, 19, 21, 26, 29
<i>Rana pipiens</i>	28
<i>Rana catesbeiana</i>	18, 19, 21-27, 29-31
<i>Gambelia wislizenii</i>	27, 28
<i>Sceloporus magister</i>	23-252, 27, 29, 31
<i>Sceloporus occidentalis</i>	16, 18, 21, 24, 25
<i>Uta stansburiana</i>	24A
<i>Cnemidophorus tigris</i>	24A, 28, 29, 31
<i>Pituophis catenifer</i>	26
<i>Thamnophis couchi</i> ¹	3, 7, 10, 11, 13, 15
<i>Thamnophis elegans</i> ²	1-5, 7, 9-15, 19-21, 26, 28

¹Subspecies: *T. c. couchi*

²Subspecies: *T. e. elegans*

although western fence lizards (*Sceloporus occidentalis*) were found upstream from Tracy Clark to site 16 (Floriston) at an elevation of 1,580 m. Because most lizards are primarily desert-dwelling animals, this distribution pattern would be expected.

Most of the 15 desert spiny (*S. magister*) and 20 western fence lizards were observed on big rocks (about one to two m in diameter) along the river. Western whiptail (*Cnemidophorus tigris*), longnose leopard (*Gambelia wislizenii*), and side-blotched (*Uta stansburiana*) lizards showed a preference for sandy or gravelly areas with scattered shrubs and/or small rocks (about 0.3 to 0.5 m in diameter).

The most widely distributed and abundant reptile observed (53 were counted) during this study was the semiaquatic western terrestrial garter snake (Table 10). It appears to be the only reptilian species that lives along the entire stretch of the river. The western terrestrial garter snake was often observed in the river (10 of 53 observations; 19%), and would often swim under rocks when pursued. It was also frequently observed near the edge of the river, especially in grassy areas with overhanging mountain alders (*Alnus tenuifolia*) or Pacific willows (*Salix lasiandra*). Of 32 observations, the average distance from the edge of the river was 3.6 m.

All 10 western aquatic garter snakes were counted in or along the upper part of the river from site 3 (near Lake Tahoe; 1,896 m in elevation) downstream to site 15 (Hirschdale Bridge; 1,659 m in elevation). This highly aquatic species (8 of 10 were observed in water; 80%) appeared to have a preference for mountain streams with a moderate rate of flow and those parts of the river with overhanging vegetation such as willows and alders. Two western aquatic garter snakes were observed in swampy, grassy areas with scattered willows.

Only one Great Basin Gopher Snake (*P. c. deserticola*) was observed during the study. This large snake (1.4 m in length) was in the river at site 26 (Wadsworth Bridge). The river at this site had a very slow rate of flow, an abundant growth of aquatic weeds, and many bullfrog tadpoles and young adults.

Current Status and Impact of Drought on Observed Amphibians and Reptiles on the Truckee River System—As long as the Truckee River maintains even a minimal flow, it does not appear that

drought conditions will severely impact existing amphibian and reptilian populations on this river system. Most of the current populations observed appear to be doing fairly well, and most of these are adapted to low-water conditions. Because the northern leopard frog was only found at one site and its distribution in this system appears to be decreasing, a concern exists for its continued survival in this river system. The distribution of the northern leopard frog also appears to be decreasing in other systems. In an unpublished manuscript, Hovingh (1990) reported that northern leopard frogs were found in only two locations in north Great Salt Lake and was not found in either Ruby Valley or Steptoe Basin where it had been reported previously in the literature. The decreased distribution of the leopard frog in the Truckee system is possibly due to success of the introduced bullfrog, which may not be compatible with the northern leopard frog. This hypothesis is supported by Moyle (1973) who reported that the bullfrog doesn't appear to be compatible with two other ranids, the red-legged frog (*R. aurora*) and the foothill yellow-legged frog (*R. boylei*). He attributed the disappearance of *R. aurora* from the San Joaquin Valley, California, and the continuing reduction in the range of *R. boylei* in this region, to habitat alteration coupled with predation and competition from *R. catesbeiana*. Additional support for this hypothesis is found in a report by the Committee on Rare and Endangered Wildlife Species, 1966. According to this report, the bullfrog was held partially responsible for the elimination of the Vegas Valley frog, *R. pipiens fisheri*. Other possible hypotheses explaining the decline of western ranids have been reported by Hayes, et al., (1986). They suggested that in addition to the introduction of bullfrogs, over harvesting (commercial exploitation), habitation alteration, and fish predation are tenable, but not necessarily exclusive, alternative hypotheses accounting for the decline of western ranids.

To determine the actual cause of the decreased distribution of the northern leopard frog in the Truckee system, more studies are necessary. A study of reintroductions of this species in portions of the river with suitable habitat that are free of bullfrogs and predatory fish appears to be a good one. Reintroduction studies should also be conducted with other ranids throughout the western United States.

There is also concern and interest about the status of the western pond turtle in this river system. Apparently, a few western pond turtles are still living in the Truckee River. In an unpublished manuscript, Holland (1991) reported a single reliable sight record for the Truckee River drainage. He checked the site and interviewed the reporting parties in 1987. Also, he reported that the turtle was a large male and probably represents one of the last of this species in this area. In 1991, Holland (unpub. manus.) also conducted extensive sur-

veys along the Truckee, but found no turtles. During this study, no turtles were observed. Thus, it appears that the remaining population of western pond turtles along the Truckee River System is extremely small.

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Fire History and Stand Development of a Douglas-fir/Hardwood Forest in Northern California

Abstract

This paper examines the relationship between historic fires and stand structure on three sites in Douglas-fir/hardwood forests within the Klamath National Forest, California. Fire scar, tree age, and basal area distributions were used to interpret stand history. Frequent fires of variable intensity resulted in varied stand structures on our study sites. Some stands were even-aged and -sized following a relatively intense fire, while others were multi-modal following moderate or low intensity fires. Stands with dominant trees 250+ years old have old-growth characteristics. These Douglas-fir dominated stands do not resemble those of western Oregon and Washington. Douglas-fir in our stands seems to respond to fire and appropriate environmental conditions for successful establishment. Stand development may be defined by coarse and medium scale gaps. Large uniform patches created by infrequent catastrophic fire are broken up by more frequent medium scale gap processes. The pre-settlement landscape was probably exceptionally patchy containing complex mosaics of different age and size Douglas-fir dominated stands.

Introduction

Fire's role in the establishment and development of Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) forests has been comparatively well-documented for northwestern Oregon and western Washington. Both north-south and west-east gradients reflect a pattern of generally increasing fire frequency and decreasing severity (Thornburgh 1969, Hemstrom and Franklin 1982, Yamaguchi 1986, Spies and Franklin 1989, Agee 1991a).

In west-central and southwestern Oregon a pattern of relatively frequent fire has been reported. These forests experience greater fire diversity ranging from infrequent stand replacing events with mean fire intervals [MFI] of 95-149 yrs (Means 1982, Stewart 1986, Morrison and Swanson 1990) to more frequent moderate or light surface fires having MFIs of 15-50 yrs (Atzet and Wheeler 1982, Agee 1991b). The ensuing stands often have more than one cohort and are multi-sized with more than one canopy layer.

Relatively little fire ecology research has been done in northwestern California Douglas-fir forests. The fire history study closest to our study sites was conducted by Adams (1980). He examined composites of Douglas-fir stumps in clearcuts on four sites from Gasquet to Mad River, California documenting increasing fire frequency with distance from the ocean and along a north to south

gradient. Mean fire return intervals ranged from 21.4 years in Gasquet (north) to 12.7 years in Mad River (south).

Our objective was to assess fire history, age structure, and stand structure in several Douglas-fir/hardwood stands. We hypothesized that dominant and co-dominant cohorts became established following either stand-replacing fire or by gap-producing moderately severe surface fire. We further hypothesized that there was a significant difference in mean fire interval across the pre-settlement (approx. 1740-1849), settlement (approx. 1849-1905), and suppression (approx. 1905-1987) time periods.

Study Area

This study was conducted within the Salmon River Ranger District of the Klamath National Forest, California. Study sites were located on Hotelling Ridge, above the South Fork of the Salmon River. Slopes averaged 56% with elevations between 900 to 980 m.

The Salmon River area has mean temperatures of 36°C in summer and 2°C in winter. Normal annual precipitation is 1120 mm, with 90% occurring between October and May (records available from the Klamath National Forest, and Six Rivers National Forest, for Orleans). Summers are long and hot, with relatively severe fire weather occurring in July, August, and September. Thunderstorms accompanied by lightning take place occasionally during the summer months. Snow may fall in early October and last until May at higher elevations.

¹Current address: The Santa Rosa Ecological Preserve, Murietta, California 92562.

²To whom reprint requests should be addressed.

Study sites were located in a Douglas-fir/hardwood forest (Bingham and Sawyer 1991) dominated by open upper canopies of Douglas-fir with scattered stems of sugar pine (*Pinus lambertiana* Dougl.). A subordinate canopy layer was dominated by tanoak (*Lithocarpus densiflora* [Hook. and Arn.] Rehd), madrone (*Arbutus menziesii* Pursh.), and canyon live oak (*Quercus chrysolepis* Leibm.). Dominant shrubs include hazel (*Corylus cornuta* Marsh.) and Oregon-grape (*Berberis nervosa* [Pursh.] Nutt.).

In late August, 1987 a series of lightning strikes ignited a complex of fires on the Klamath National Forest. These fires spread quickly and extensively, having variable intensities, but often burning into the crowns of stands of all tree sizes. A total of 110,000 ha burned. One of the Klamath complex fires, the Yellow Fire, burned on Hotelling Ridge and killed the majority of trees within the study plots. Salvage logging occurred in 1988 and 1989.

Methods

Three study sites were selected. Each site was considered to be visually representative of stand conditions in the area. Stands selected were consistent in aspect, slope, elevation, and dominant canopy trees. Examination of stumps showed abundant evidence of previous fires. Study sites ranged from 5 to 8 hectares. Site 1 and Site 2 were separated by approximately 0.5 km with Site 3 being 1.0 km west of Site 2.

Fire scar and tree age class data were obtained from Douglas-fir and sugar pine stumps. Three 30m diameter circular plots were established within each site. Stem cross-sections were collected from all stumps within plot boundaries. In addition, stem cross-sections were gathered from all other fire-scarred conifer stumps within the study site. All cross-sections were cut with a chain saw at an approximate height of 30 cm. Hardwood specimens were not collected because their poor condition made accurate determination of fire scar dates and tree ages impossible.

Cross-sections were prepared with a power planer and subsequently polished with a rotary sander. Successively finer grits of sandpaper, down to 360, were used to render an easily readable surface. Following preparation, the samples were examined using both a hand lens and a binocular microscope. Annual ring counts were made on one or more radii, depending on growth and ease of

interpretability. Tree diameters were measured from prepared specimens and fire scar dates recorded. Fire scars were recognized using criteria described by McBride (1983).

Cross-dating of tree rings (Stokes and Smiley 1968) wasn't possible with most specimens, presumably because competition influenced radial growth more than climate. Scarring dates were affixed for fire scars on stumps with indeterminable 'bark' dates by matching fire scar intervals with those on stumps of known age. Established fire scar dates of all trees within a site were collated into a master fire chronology. Less reliable fire scar dates were adjusted using the techniques described by Arno and Sneek (1977). No scar date was adjusted more than ± 3 years. Only confirmed fire scar dates were used to calculate mean fire intervals.

Statistical Analysis

Descriptive statistics were used to report age structure, size structure, and fire history. We used inferential statistics to detect differences in mean fire interval across study sites and across time periods. We used multiple Kruskal-Wallis non-parametric tests on our data in lieu of analysis of variance because of untransformable heteroscedasticity.

Results

Fire histories varied among the three sites (Table 1). Four fires occurred on both sites 2 and 3; 1987, 1870, 1795, 1776. The 1987 fire was the only one to have occurred on all the sites. Site 1 also shares the 1849 fire with site 3. Table 2 lists mean fire intervals for the pre-settlement, settlement, suppression periods. There was no significant difference in mean fire interval between sites ($p = 0.388$), but there was a significant difference between periods ($p = 0.033$). The suppression period had significantly longer MFIs than the settlement and pre-settlement periods combined ($p = 0.010$), but there was no significant difference between the settlement and pre-settlement periods ($p = 0.686$).

The age of Douglas-fir stumps ranged from 47 to approximately 520 years, while sugar pine ages ranged from 60 to 251 years. The first twenty years of radial growth varied from 0.32 mm/yr, among highly suppressed trees on site 2, to 2.20 mm/yr among individuals established following a stand replacing fire in the late 1800's on site 1.

TABLE 1. Master fire chronology for study sites. Number of fire-scarred trees are listed by plot for each date.

Date	Site 1	Site 2	Site 3						
	Plot A	Plot B	Plot C	Plot A	Plot B	Plot C	Plot A	Plot B	Plot C
1987									
1944	1	1							
1942					2				
1919				3					
1916								1	
1913								2	
1901					2				
1894		1	5						
1890				1	6	2			
1888									1
1882					2				
1870				1	10			1	
1868	1								
1862				1	6				
1860	1								
1855				2	4				
1854								2	
1849	1	1						2	
1842				1	1				
1839				2	3				
1835							1	1	
1834				1	1				
1828					4				
1820	2								
1818				1	4				
1811					1				
1810								2	
1806				1	2	1			
1797	1		1						
1795					4			5	
1785					1	1			
1783								1	
1776					4				1
1760					4				
1759							1		
1756			2						
1752								3	
1750	1	1							
1745	1	1							
1742				1	1				

Site 1 had two well-defined even-aged cohorts (Figure 1) in plots B and C. Two of the oldest individuals in Plot A germinated within 12 years of each other and may represent the remnants of an older cohort. Of the remaining 3 individuals, two trees have ages correlated with the two well-defined regeneration cohorts of plots B and C. Trees in plot B were mostly associated with the cohort which became established in about 1722. Individuals sampled in plot C were established over a 40 year period between 1892-1932.

Each of the plots in site 2 had well defined regeneration cohorts (Figure 2). The majority of

older trees in plot A originated following an apparently high intensity, stand replacing fire around 1802. Only two trees, established in 1582 and approximately 1473 survived this fire. Four surviving trees were established, at even intervals, between 1837 and 1887. A second regeneration cohort began in about 1895. Plot B had a bi-modal age distribution, with the oldest trees germinating between 1717-1722. Establishment lasted approximately 50 years. Only one surviving tree was established between 1770 and 1910. Understory trees germinated after 1910 with regeneration continuing for 40 years. Plot C also had a bi-modal

TABLE 2. Means and ranges of fire intervals for each site. Data are reported for the pre-settlement, settlement, and suppression periods as well as for the complete chronology. Data are in years.

Site	Interval	Mean	Range
Site 1 (N = 11)			
Complete chronology	1745-1987	22.0	5-50
Pre-settlement	1745-1849	17.3	5-41
Settlement	1849-1894	15.0	8-26
Suppression	1894-1987	46.5	43-50
Site 2 (N = 19)			
Complete chronology	1742-1987	12.9	5-45
Pre-settlement	1742-1855	10.3	5-18
Settlement	1855-1901	9.2	7-12
Suppression	1901-1987	28.7	18-45
Site 2 (N = 13)			
Complete chronology	1752-1987	18.1	3-71
Pre-settlement	1752-1849	13.9	7-25
Settlement	1849-1913	16.0	5-25
Suppression	1913-1987	37.0	3-71

age distribution, but with only one third the tree density of plot B.

The age structure of combined plots in site 3 exhibited a bi-modal distribution (Figure 3). Plots A and C had single regeneration cohorts apparently initiated by a stand replacing fire in the late

1800's. Surviving seedlings in plot C became established over a 35 year period, while the regeneration period in plot A lasted 50 years. Dominant trees in plot B survived the late 1800 event which replaced stands in plots A and C. Plot B's age distribution may be best described as having occasional seedling establishment since 1800 with a well-defined cohort spanning 40 years centered in 1757.

Site 1 had an average of 54.6m²/ha of basal area with site 2 having 72.9m²/ha and site 3 having 38.4m²/ha. Each plot in site 1 had only one dominant cohort (Figure 1). The greatest basal area was concentrated in the dominant age cohort of plot B, centered around 1735.

Plot B of site 2 had more basal area then either plot A or plot C (Figure 2). Even though plot B has a bi-modal age distribution, it was overwhelmingly dominated by the cohort established in the mid-1770s. Plots A and C had relatively small basal areas spread across several cohorts.

A bi-modal distribution of basal area was found in site 3. Two groups can be distinguished among plots A and B and plots A and C. Basal area values were low, particularly for plots A and C.

Discussion

Mean fire return intervals resulting from this study further substantiate the trend for shorter MFIs in

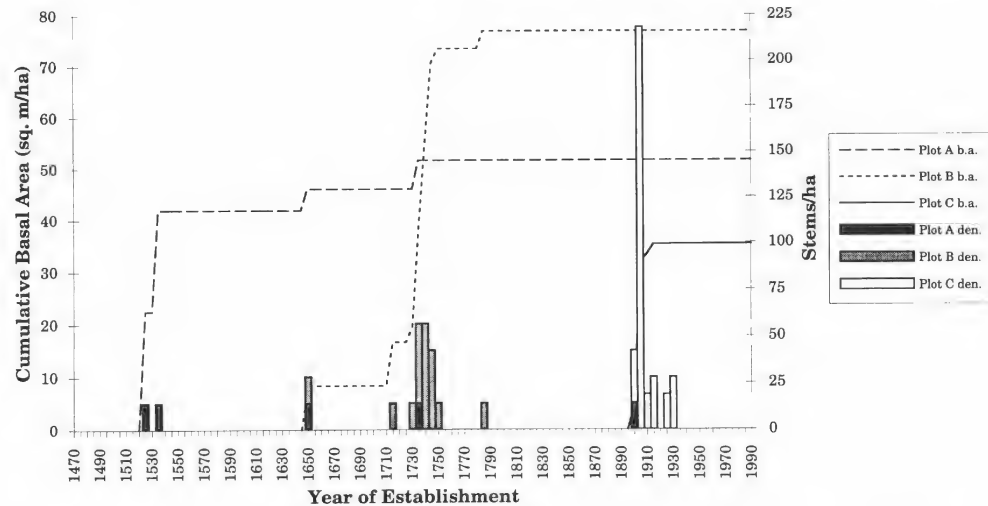


Figure 1. Age class and cumulative basal area distributions of trees established prior to the 1987 Yellow Fire from site 1, plots A-C. Data are compiled in 5-year classes.

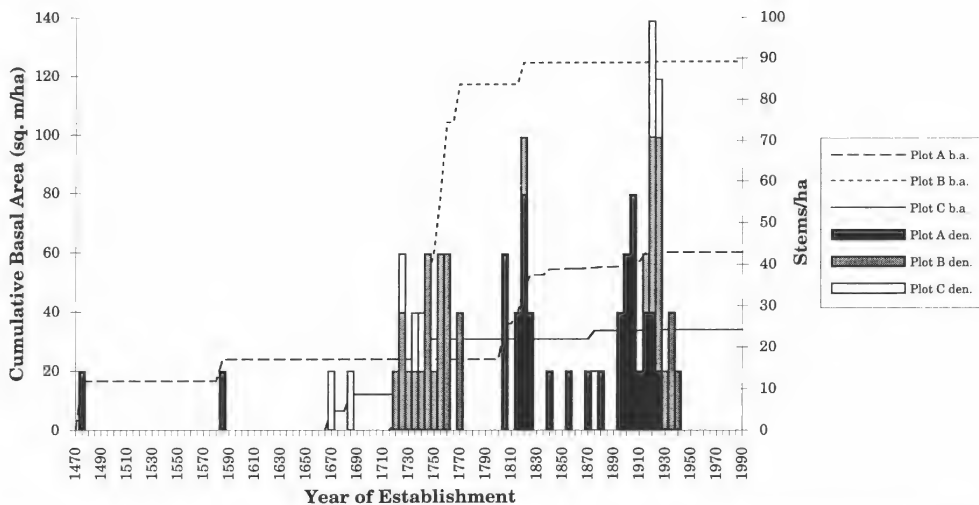


Figure 2. Age class and cumulative basal area distributions of trees established prior to the 1987 Yellow Fire from site 2, plots A-C. Data are compiled in 5-year classes.

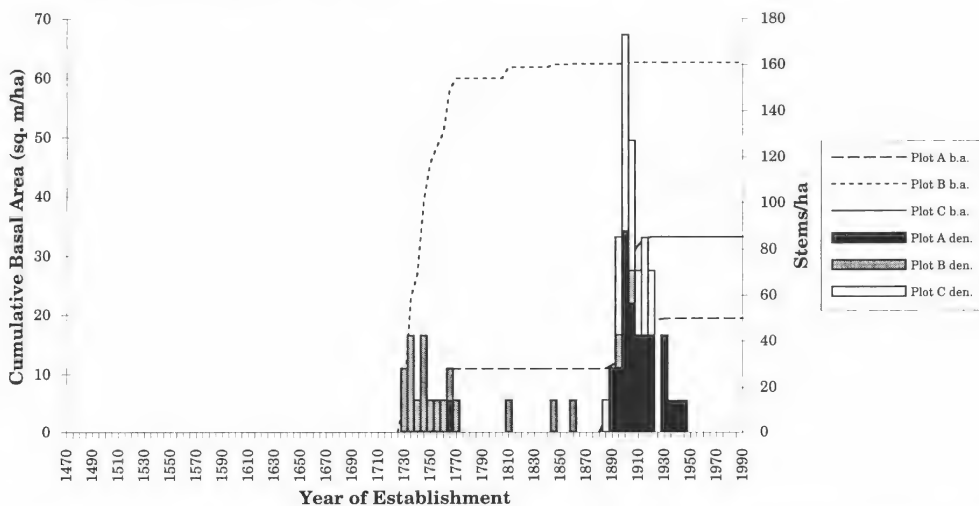


Figure 3. Age class and cumulative basal area distributions of trees established prior to the 1987 Yellow Fire from site 3, plots A-C. Data are compiled in 5-year classes.

the southern range of Douglas-fir. Our pre-suppression mean fire intervals of 10 to 17 years were considerably shorter than the 15-50 yr range reported for southern Oregon (Atzet and Wheeler 1982, Agee 1991b) and the 95-149 yr range in west-central Oregon (Means 1982, Stewart 1986, Morrison and Swanson 1990).

Our fire-free intervals were similar to those reported for mixed conifer forests in the Sierra Nevada (Show and Kotok 1924, Wagener 1961, Kilgore 1973). Reasons for this include comparable summer fire weather and sub-canopy and understory layers having sclerophyllous, pyrolytic species.

Natural establishment and survival of Douglas-fir on these sites was only occasionally successful. The combination of factors necessary for success may be relatively rare. Establishment may follow a pattern similar to that found in southwestern ponderosa pine (*Pinus ponderosa* Laws.). Cooper (1961) and White (1985) found that successful ponderosa pine regeneration was mainly dependent on appropriate soil moisture conditions and seed-bed availability. Similar conditions may be prerequisite for successful Douglas-fir establishment on our sites. Douglas-fir's shade intolerance (Minore 1979) and need for mineral soil or burned seed beds (Stewart 1986) may explain the episodic pattern of regeneration on the sites examined in our study.

Age class distributions indicated that seedling establishment occurred frequently enough to allow perpetuation of these Douglas-fir dominated forests. On our sites, forest fires on about a 140 year interval provided sufficient growing space for the initiation of patches of Douglas-fir. On some plots it appeared that no residual trees survived fire, while on others the apparent fire severity was low enough to allow the survival of some overstory trees. The resulting multi-aged structures resembled those found in the Oregon Cascades (Means 1982). In our study, even-aged groups became established following liberation of growing space by moderately severe forest fires. Size distributions of these stands and fairly long recruitment periods account for the mosaic of even-aged groups of trees established after fires.

Age class distributions in plots on our sites were uni-modal or bi-modal. Similar patterns have been described in developing Engelmann spruce (*Picea engelmannii* Parry ex Engelm.; Day 1972, Whipple and Dix 1979) and Douglas-fir (Stewart 1986) stands. In these studies, deviation from a negative exponential size distribution was correlated with the spatial scale of disturbance and gap formation. Cumulative age and size curves are shaped at least as much, if not more by establishment patterns as by mortality (Parker and Peet 1984). The high fire frequency on our sites may inhibit the development of negative exponential size distributions.

Douglas-fir dominated stands in Idaho and Montana have been reported to be initially even-aged (Larson 1925, Shearer 1976, Tesch 1981). This was also true for some plots within our study sites. Full site occupancy by Douglas-fir was probably reached in 15 to 50 years following distur-

bance. Similar time periods were found in Douglas-fir forests of Oregon and Washington (Isaac 1943, Oliver 1981, Agee 1991a,b). Other workers have indicated that 60 to 150 years are required for full occupancy of Douglas-fir dominated mesic sites (Franklin and Waring 1980, Franklin and Hemstrom 1981, Means 1982). A shorter stand initiation phase may be expected in the southern range of Douglas-fir (Agee 1991a).

Site 2 had the greatest basal area. This is probably due to site 2 having fewer overstory killing fires and therefore more older trees. Frequent low severity surface fires may have also contributed to greater basal area by reducing competition for surviving overstory trees. In contrast, most of the basal area in site 1, plot C and site 3, plots A and C was associated with relatively young trees. It is likely that these ecologically dominant cohorts became established following fires intense enough to kill both the understorey as well as most of the overstorey.

Understoreys of Douglas-fir had been reinitiated on site 2 and site 3. Six of the nine plots examined had little or no regeneration present for periods of up to 240 years. Two explanations are possible for this condition. First, growing space may have been dominated by the first tree species to regenerate following disturbance (Egler 1954). In our stands, invading shrubs and residual hardwoods were likely early dominants following fire (Stuart *et al.* 1993). Shorter mean fire intervals, like those of site 2, may have favored establishment of Douglas-fir, because of the possible elimination of stored seed and residual sprouts of hardwoods. A second possibility is that higher intensities of the 1987 fire were experienced on sites 1 and 3 consuming all Douglas-fir seedling or saplings that may have been present, making them unavailable for sampling.

Spies and Franklin (1989) described gap dynamics in Pacific Northwest Douglas-fir forests, characterizing gaps as coarse or fine in scale. They defined coarse-scale gaps as having originated from large scale disturbances and as having relatively uniform even-aged stands of Douglas-fir. Fine scale patches result from small scale mortality such as self-thinning or pathogen infection. A forest subjected to fine scale mortality for a long enough period of time will result in a mosaic of openings and size classes typical of multi-aged stands.

The stands in our study differ from either alternative described by Spies and Franklin. Our

data, instead represents a third gap type that can be characterized as medium scale resulting from low to moderate severity fires following a stand replacing disturbance. These fires left much of the Douglas-fir canopy intact and inhibited the progression towards fine scale dynamics by periodically killing small trees. The age distribution of these forests are the effect of both fire and stand development. As a result, the age structure in our stands is multi-modal and correlated with fire events rather than being all aged.

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Robert E. Keane, USDA Forest Service, Intermountain Research Station, Intermountain Fire Sciences Laboratory, P.O. Box 8089, Missoula, Montana 59807

Penelope Morgan, Department of Forest Resources, University of Idaho, Moscow, Idaho 83843

and

James P. Menakis, USDA Forest Service, Intermountain Research Station, Intermountain Fire Sciences Laboratory, P.O. Box 8089, Missoula, Montana 59807

Landscape Assessment of the Decline of Whitebark Pine (*Pinus albicaulis*) in the Bob Marshall Wilderness Complex, Montana, USA

Abstract

Whitebark pine (*Pinus albicaulis*) provides important food for wildlife and important cover for snow retention and watershed protection in high-elevation ecosystems of the northwestern United States. In the northern Rocky Mountains, this species is being reduced at accelerated rates by blister rust (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*), and advancing succession resulting from fire exclusion. This study evaluates the extent and severity of the decline of whitebark pine in the Bob Marshall Wilderness Complex (BMWC) of Montana. Results of an extensive field survey of various whitebark pine communities were used to evaluate past and current whitebark pine population levels. Satellite imagery (LANDSAT TM) data were used in conjunction with field data to classify 14 BMWC subalpine cover types and 3 forest decline classes to detect extent of whitebark mortality in the study area. Results indicate whitebark pine population levels are rapidly decreasing, mostly as a result of the exotic disease blister rust. Field results show 83% of the 2,503 sampled whitebark pine trees are infected with blister rust and an average of 33% of their crowns have been killed by the disease. Results of the satellite image classification show whitebark pine dominant on 56% of the 311,257 hectares comprising the BMWC subalpine analysis area. Subalpine fir dominated a high proportion (14%) of this landscape, about 7% greater than its historical landscape composition. Approximately 22% of this landscape containing whitebark pine is now experiencing high mortality and 39% is experiencing moderate mortality. Classification accuracy was 60% for the vegetation cover types and 78% for the forest decline classes.

Introduction

Whitebark pine (*Pinus albicaulis*) is an important species of northern Rocky Mountain high elevation forests. In Montana, Idaho and northwestern Wyoming, it has been an important component on about 10-15% of the forested landscape (Arno and Hoff 1989). Although it has limited use as a commercial timber species, whitebark pine produces seeds that are highly valued by many species of wildlife as an important source of food. These animals include black bears (*Ursus americanus*) and grizzly bears (*Ursus arctos horribilis*) (Kendall 1980, Mattson *et al.* 1991), red squirrels (*Tamiasciurus hudsonicus*) (Ferner 1974) and Clark's nutcrackers (*Nucifraga columbiana*) (Tomback 1982). The nutcracker plays a mutualistic role in the whitebark pine regeneration process because it is essentially the only dispersal vector for the heavy, wingless whitebark pine seed (Tomback 1982). Whitebark pine also protects snowpack in high elevation watersheds and delays snowmelt (Arno and Hoff 1989, Hann 1990).

Whitebark pine is rapidly decreasing in some subalpine landscapes in the northern and western

part of its geographical range (Ciesla and Furniss 1986, Keane and Arno 1993, Arno 1986, Kendall and Arno 1990). This decline is a result of three factors acting separately or in concert: (1) mountain pine beetle (*Dendroctonus ponderosae*), (2) successional replacement by more shade tolerant conifers, and (3) white pine blister rust (*Cronartium ribicola*). Mountain pine beetle epidemics killed many mature whitebark pine trees during the 1940's (Baker *et al.* 1971). The successional replacement of whitebark pine by subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) is a process that is usually retarded by naturally occurring fires. However, 60 years of fire suppression combined with mountain pine beetle and blister rust attacks have allowed fir and spruce to become dominant in forests historically dominated by whitebark pine (Arno 1986). Blister rust, an exotic disease from Europe introduced in the western United States in 1910, is especially fatal to whitebark pine when compared to other 5-needle pines (Arno and Hoff 1989, Bedwell and Childs 1943, Bingham 1972, Hoff and MacDonald 1977, Hoff *et al.* 1980).

The extent and severity of whitebark pine's decline across its range are poorly documented. Whitebark pine's low economic importance coupled with its inaccessible habitat have contributed to a lack of inventory and research data for this species. Most information has been from casual site observations rather than from extensive scientific surveys or investigations across entire landscapes. This study was initiated to determine the status of whitebark pine populations across the Bob Marshall Wilderness Complex, a large wildland preserve in northwest Montana. Subalpine forest communities were intensively inventoried to develop a spatial classification of cover types and forest decline classes using data from satellite imagery.

Satellite imagery has been used to classify existing vegetation and evaluate forest damage. Identification of vegetation cover types is best accomplished using the visible, near-infrared and mid-infrared spectral region of solar radiation (Jensen 1986, Moore and Bauer 1990, Bolstad and Lillesand 1992). Defoliation by gypsy moth (*Lymantria dispar*) has been detected using LANDSAT Thematic Mapper (TM) and SPOT data (Joria and Ahern 1991, Ambrosia *et al.* 1990). Trees damaged by spruce budworm (*Choristoneura fumiferana*) have been mapped by Leckie and Ostaff (1988) using satellite imagery. Various types of remotely sensed imagery was used to document forest decline in Europe and the state of Vermont (Kenneweq 1989, Landauer 1989, Rock and Vogelmann 1989, Vogelmann and Rock 1986).

Spectral reflectance shifts markedly as a result of insect damage on balsam fir (*Abies balsamea*) and lodgepole pine (*Pinus contorta*) (Leckie *et al.* 1988, Ahern 1988). Stressed and dying trees show a difference in reflectance in the red, near-infrared and thermal region as compared with healthy trees (Ahern 1988, Rock *et al.* 1986, Puritch 1981, Rock and Vogelmann 1989). Spectral wavelengths most sensitive to the detection of foliage mortality seem to range from 500 nm to 660 nm and 770 nm to 1600 nm which approximately encompass TM bands 2-5 (Ahern 1988, Leckie *et al.* 1988, Joria and Ahern 1991). Wavelengths in mid-infrared and thermal regions (TM bands 7 and 6) have been used for forest damage detection with limited success (Leckie and Ostaff 1988). Wavelengths in these regions include emitted radiation and are used for mortality classification because they often detect woody debris accumulation

such as dead snags and downed logs (Elvidge 1988).

Study Area

The Bob Marshall Wilderness Complex (BMWC) is a remote 600,000 hectare preserve in northwest Montana, USA, composed of the Great Bear, Bob Marshall and Scapegoat Wilderness Areas (Figure 1). This area consists of mountainous terrain dissected by major river drainages. Two periods of glaciation formed the rugged cirque and peak landscape and filled valley bottoms with loosely consolidated glacial outwash alluvium (Alt 1985, Deiss 1958). Parent material is mostly quartzite and argillite with alternating layers of limestone, mostly in the eastern portions (Alt 1985). The Continental Divide is a high mountain barrier that transects the wilderness creating a unique blend of climates and plant communities. The climate west of the divide is modified maritime with cool wet winters and short, warm-dry summers. Average annual precipitation ranges from 50 cm/year in the driest valleys to over 275 cm/year on the Swan Front (the westernmost mountain range). East-side climates are continental with widely fluctuating winter temperatures and warm dry summers. Consistent winds are common along the east side of the Continental Divide. Precipitation averages 40 cm/year in the valleys to 150 cm/year along the Sawtooth Range (Soil Conservation Service 1981).

Whitebark pine is a major seral species at elevations above 1,830 meters within the study area. It has the potential to dominate 35-45% of the subalpine landscape within the BMWC (Bain 1990). In the absence of disturbance, whitebark pine is eventually replaced by the more shade-tolerant subalpine fir and Engelmann spruce in most of the area but it can form nearly pure climax stands on some high, dry ridges and mountain tops (Pfister *et al.* 1977).

Fires were common on the BMWC landscape during the last four centuries. Ayres (1901) estimated 20-40% of BMWC's whitebark pine forests burned during 1860 to 1900. Large, stand-replacement fires are typical in the study area, especially in the whitebark pine zone (Losensky 1990). The great dispersal distances of the nutcracker allow whitebark pine a competitive advantage in colonizing large burns (Tomback *et al.* 1990). Also, Clark's nutcrackers prefer open, burned areas to cache whitebark pine seeds

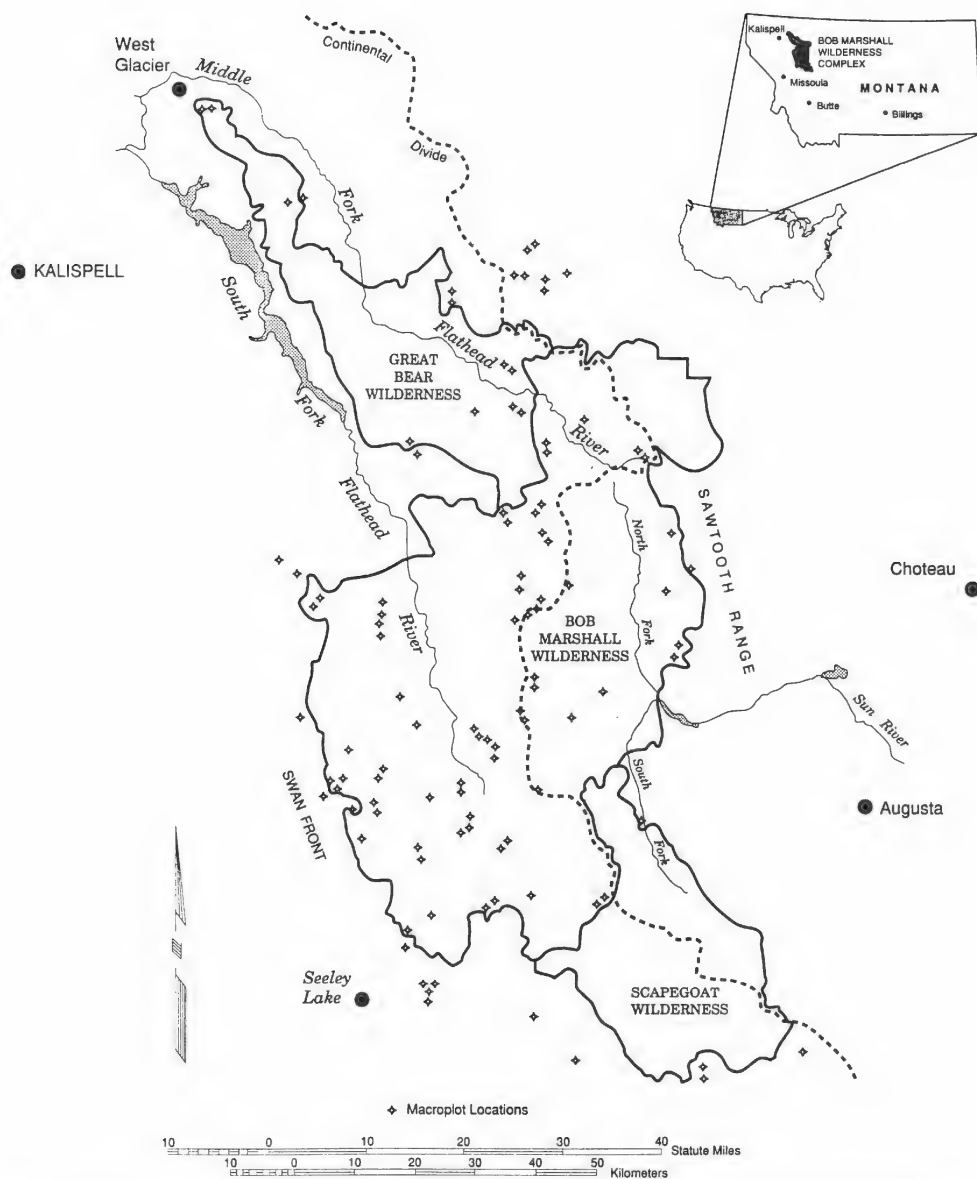


Figure 1. Map of the Bob Marshall Wilderness Complex in west-central Montana, USA with locations of macroplots sampled for this study.

(Tomback *et al.* 1990). Some whitebark pine stands in higher and drier areas of the southern portion of the BMWC contain evidence of less severe, more frequent surface fires (Gabriel 1976). These fires tend to kill mostly subalpine fir which

favors the somewhat fire-resistant whitebark pine (Arno 1986). As a result, these fires maintain whitebark pine dominance and eliminate the subalpine fir understory (Arno and Hoff 1989).

Methods

Field Data Collection

A detailed ecological inventory was conducted in various whitebark pine stands across the entire BMWC and surrounding areas using ECODATA methodology (Keane *et al.* 1990, Hann *et al.* 1989). Circular 400 m² macroplots were located in representative portions of stands where whitebark pine had a density greater than 10 mature (greater than 15 cm diameter at breast height—DBH) trees per ha. Stand structure, fire history, fuels, topography, soils and plant community information were recorded at each macroplot. All trees greater than 2 cm DBH were sampled for age, size, and health. Fire scars on trees and tree ages were collected to obtain a fire history for the study area (Arno and Sneek 1977). Down, dead woody fuels (twigs, branches and logs) and organic matter (duff and litter) characteristics were inventoried about the macroplot using planar techniques (Brown 1974). Macroplots were geographically referenced using a Global Positioning System (GPS) to link these data to satellite imagery for development of spectral classifications.

Blister rust severity was evaluated for each whitebark pine tree as an estimation of (1) number of cankers per tree, (2) number of infected trees within the macroplot and (3) proportion of tree foliage killed by the rust. The number of

cankers visible from the ground were estimated into broad classes (0 to 5, 5 to 10, and so on). The number of infected trees and the proportion of rust-killed foliage were ocularly estimated. Presence of mountain pine beetle was also recorded for each whitebark pine snag and living tree. Causes of mortality were estimated for dead trees when evidence existed.

Image Processing and Classification

Cover type and forest decline class for all BMWC subalpine and alpine areas were classified using satellite imagery in conjunction with digital terrain and environmental data (e.g., elevation, aspect, slope, estimated annual precipitation and vegetation type) (Figure 2). The GRASS spatial software package was used to analyze and classify the satellite imagery and manage the spatial data layers in a Geographic Information System (GIS) (USA CERL 1990). The Flathead and Lewis and Clark National Forests supplied many of the GIS layers used in TM classification analysis including previous vegetation classifications from LANDSAT Multispectral Scanner (MSS) scenes done in the late 1980's (Bain 1990).

A late summer 1990 September 3 LANDSAT Thematic Mapper (TM) scene (ID Y5237717443X0, Path 41, Row 27) was purchased for this classification effort. All seven spectral bands that comprised the TM scene were

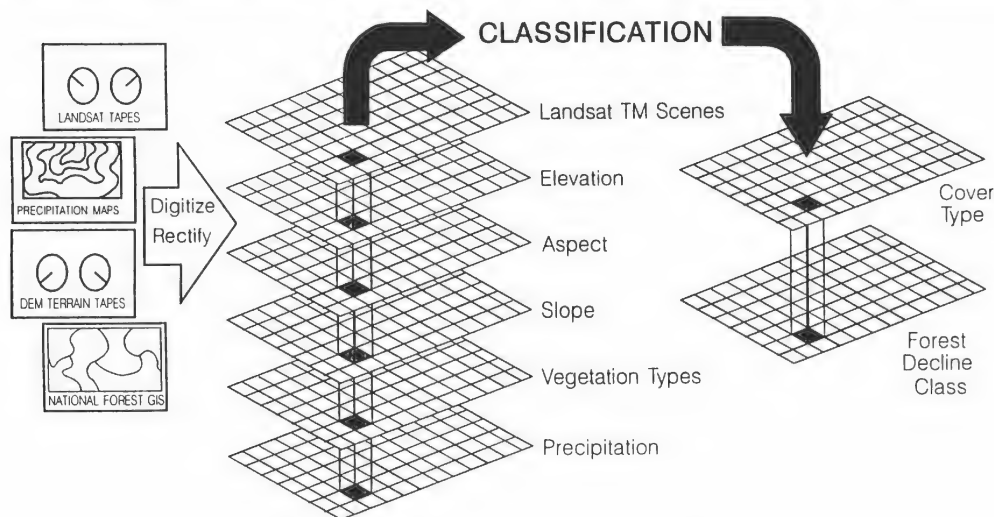


Figure 2. Procedure used to classify LANDSAT TM imagery to cover type and forest decline classes.

included in the analysis. A TM spectral band is composed of a matrix of 30 x 30 m pixels with each pixel's digital value representing the reflectance of light between a range of wavelengths integrated across the pixel area. However, the thermal TM band 6 had a pixel size of 120 x 120 m and detects mostly emitted radiation. TM band 7 also contains some emitted energy.

The TM scene needed some preprocessing before it was used to classify vegetation. First, all bands were geometrically rectified to the Flathead National Forest GIS layers using a coordinate transformation function in GRASS (*i.rectify* command) (RMS error = 19.46 meters or 0.65 pixel resolution). Next, the digital values for all seven bands of the TM scene were then radiometrically converted to radiance using gains and bias supplied by EOSAT (Price 1987, Leprieur *et al.* 1988). These radiance data were then corrected for haze and atmospheric effects (Jensen 1986) and included as layers in the BMWC GIS as supplied by the National Forests.

Many portions of the BMWC were excluded from the classification analysis. The TM scene covered only the central portion of the BMWC, missing most of the Scapegoat and Great Bear Wilderness areas (about 25% of the total BMWC land area). As a result, only areas within the boundaries of the BMWC and the image were considered in the classification analysis area. In addition, all areas below 1,830m in elevation, about 28% of the remaining analysis area, were excluded from the analysis because intensive field observations, including those from this study, indicate whitebark pine is seldom a major forest component below this elevation in the BMWC (Arno and Hoff 1989, Bain 1990, Pfister *et al.* 1977). Large geographic features such as lakes, marshes, ice and persistent snowfields delineated in the National Forests' GIS layers were also removed from the analysis (about 1% of the remaining BMWC analysis area). The final analysis area contained 51% of the total BMWC land area or 311,257 hectares and is shown in Figure 3.

Approximately 800 historical ECODATA macroplots that were used to develop past MSS vegetation classifications in the study area served as additional ground truth for this study's cover type classification. These macroplots were especially useful for characterizing those cover types that did not contain whitebark pine (Bain 1990). None of the historical ECODATA macroplots contained tree

health or mortality information so they could not be used in the forest decline classification. Approximately 262 of the historical macroplots and 11 of this study's ECODATA macroplots were randomly excluded from the classification effort so they could be used as tests of the final classifications.

A preliminary cover type classification of all macroplots using the ECOPAC software package (Keane *et al.* 1990) identified 14 cover types and 3 forest decline classes important on the BMWC subalpine landscape. Gradient analysis techniques such as ordination with the programs TWINSpan and DECORANA (Hill 1979a, Hill 1979b) were used as aids in the cover type classification effort (Gauch 1982). Environmental gradients interpreted from ordination results were used as guidelines for plot classifications. Plots were classified into cover types based mostly on the overstory dominance of tree species canopy cover. Cover types were named for the three dominant tree species in order of importance. For example, cover type 1 was dominated by whitebark pine (30% canopy cover), with minor amounts of subalpine fir and Engelmann spruce (17 and 10%, respectively). Next, 110 macroplots were selected from all macroplots used in this classification to best represent every cover type and decline class on the ground. A minimum of 2 macroplots were used to represent each cover type, and a minimum of 20 macroplots represented each forest decline class. These selected macroplots then defined the training sites used in the TM scene supervised classification effort (Jensen 1986). Training sites are composed of a 3 x 3 pixel buffer around a central pixel that is the macroplot location. A digital color composite created from the TM spectral data was used to expand some training site boundaries. Macroplots not selected for use as training sites were used in the test of the TM classifications.

Supervised techniques were used to derive spectral signatures for the spatial classification of the TM scene from training site radiance values (Jensen 1986). Spectral signatures are composed of the mean values for each TM band and their associated variances and covariances computed across all pixels within a training site. Classified layers for cover and forest decline type were created by using the GRASS maximum likelihood algorithm (*r.maxlik* command) to classify each pixel from the spectral signatures of the training sites and the TM spectral data (USA CERL 1990).

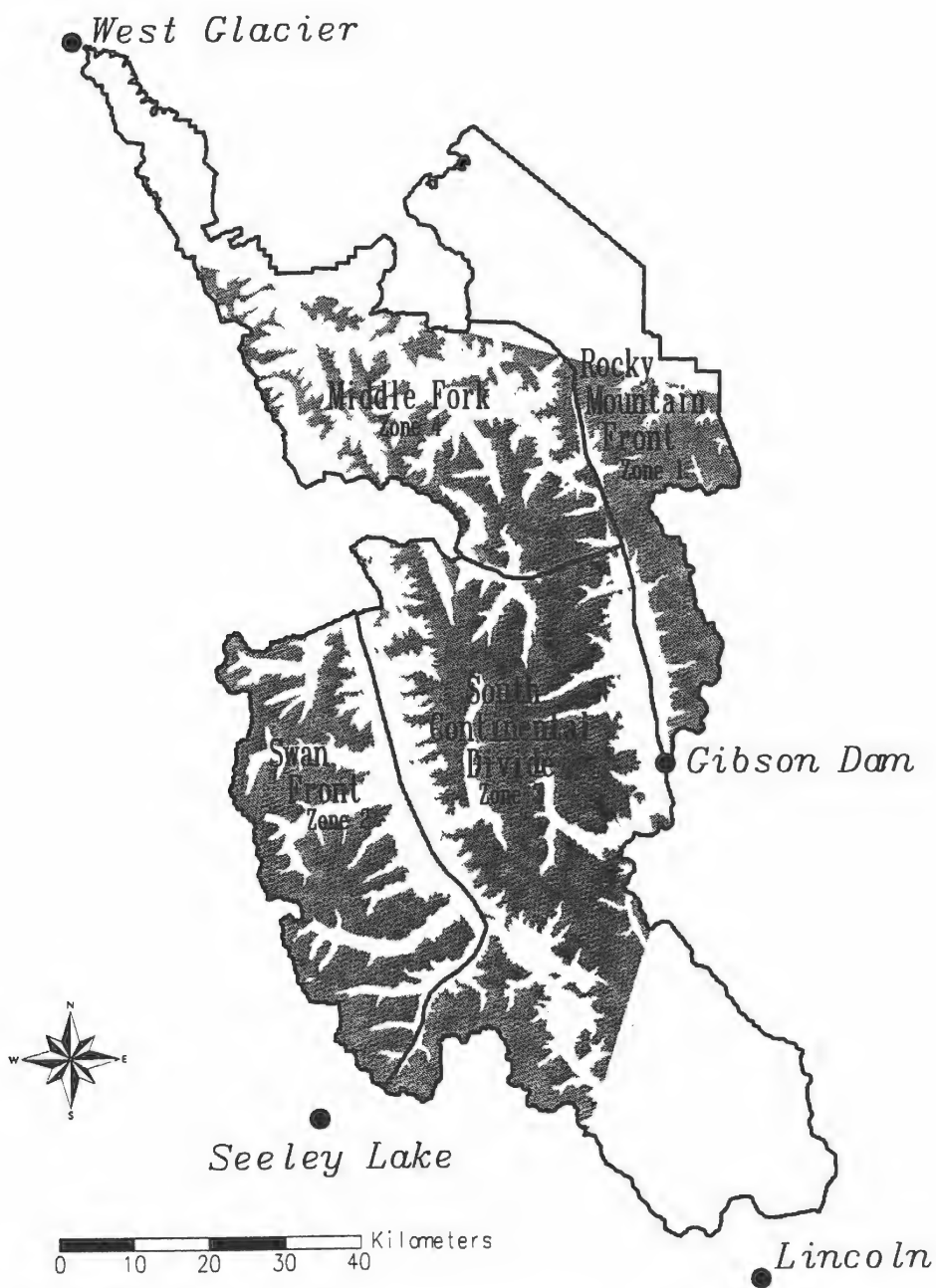


Figure 3. The BMWC image classification analysis area (shaded area). This portion of the study area includes only land covered by the TM scene that is above 1830 meters elevation. Also shown are the four BMWC geographical zones used to stratify research results.

These classified layers were then passed through a coarse-level filter to "smooth" the classification and remove "noise" generated from the input data and classification algorithm (Jensen 1986, Schowengerdt 1983). This filter was a 5 x 5 pixel window with the central pixel assigned a class value equal to the modal value of surrounding 24 pixels. The purpose of this low-pass filter was to achieve a minimum patch size of 0.1 ha commonly observed on the BMWC subalpine landscape.

Various combinations and transformations of the seven TM spectral bands were used to detect subtle characteristics in cover and forest decline type for the classification. Different combinations of TM bands (e.g., 3,4,5,7 is a TM band set) were used to achieve the best cover type and decline classification. Normalized difference vegetation index (NDVI) transformation was also included in TM band sets to distinguish cover type. NDVI is the ratio of the difference in band values and the sum of band values of the red and near infrared TM bands ($\text{Band 4} - \text{Band 3} / \text{Band 4} + \text{Band 3}$) (Perry and Lautenschlager 1984, Jensen 1986). Principal Components Analysis (PCA) was performed on the seven TM bands using the GRASS software to reduce the dimensionality of the TM band set by compressing the information content of the seven bands into three principal component images (Jensen 1986, Schowengerdt 1983). Canonical Components Analysis (CCA) was also performed on TM bands 1-5 and 7. CCA is implemented in the GRASS program *i.cca* that takes the TM band data and a signature file containing the means and variance-covariance matrix of several training sites and creates transformed raster band files that provide maximum separability between training sites (USA CERL 1990). Three training sites from each of the identified 14 cover types were randomly selected for use in CCA transformation from the total of 110 possible training sites.

Elevation, aspect, slope and average annual precipitation spatial information from the GIS were used to refine the spectral classification of those pixels that were poorly classified based on a chi-square test of the classification results (Figure 2) (USA CERL 1990). Pixels not classified by the maximum likelihood algorithm to within a 20% chi-square confidence interval were then assessed for placement into another class based on topographical criteria taken from the macroplot data. A heuristic rule-based decision system that keyed

cover type from the topographical and climate information was implemented for this effort using the GRASS command *r.infer* (USA CERL 1990). Relationships of classified cover types to topography and climate were taken from sampled macroplot information and ecological studies (Pfister *et al.* 1977, Arno and Hoff 1989). The previous MSS vegetation classification of the BMWC was also used in this classification's refinement to assess general trends of the poorly classified pixels. An ecological description of each classification category was summarized from the macroplot data using the ECOPAC software package (Keane *et al.* 1990). Characteristics that describe cover types or forest decline classes were computed as an average and range across all macroplots assigned to that class category (Jensen 1986). Only those areas classified to cover types containing whitebark pine were used to classify forest decline.

The final classified cover type layer was tested for accuracy after the filter smoothing using the ECODATA macroplots excluded from the classification effort. A 3 x 3 pixel boundary around each macroplot location was used as reference in the test procedure yielding nine test pixels per macroplot. The test involved overlaying the classified layer on the nine pixel macroplot reference stands to evaluate how the reference pixels matched the classified pixels. The same method was used to test the final forest decline classification but only the macroplot data taken for this study was used because historical macroplot information did not include adequate rust and tree mortality evaluations.

Results

Field Study

Over 2,500 whitebark pine trees were individually sampled from 111 whitebark pine stands established across the entire BMWC (Figure 1). Typically, sampled stands consisted of an overstory of old whitebark pine and spruce (20 to 500 trees/ha, 258 to 489 years of age) with an understory of almost exclusively subalpine fir (8 to 5,000+ trees/ha, 30 to 250 years of age). Only ten plots contained any whitebark pine regeneration (less than 50 years old). Whitebark pine snags were common ranging from 0 to 123 trees/ha. No evidence of extensive beetle epidemics was observed in the study area.

Blister rust is responsible for the majority of whitebark pine mortality in the BMWC. It was

present in all but 3 of the 111 sampled stands. Blister rust had infected an average of 83% of the living whitebark pine trees and these trees had 10 to 15 cankers. An average of 33% of the crown of all living trees was killed by the rust. Field data suggest blister rust is prevalent over the entire BMWC with the highest incidences observed in the northern and western portions (Table 1). The southern portion of the Continental Divide in the BMWC seems to have lower blister rust severity.

TABLE 1. Field results of blister rust severity by geographical region within the study area. Severity is expressed as a percent of total live trees infected with rust, mean number of cankers per tree by class, and mean percent of crown killed by rust for whitebark pine trees on the macroplots.

Geographic region	Number plots	Percent trees infected	Average cankers/tree	Percent crown kill
Swan Front	39	92	11-15	41*
Continental Divide	35	67*	6-10*	15*
Sawtooth Range	18	86*	11-15	33*
Middle Fork	19	93	11-15	48*
Averages	28	83	11-15	33

*Significant at $p=0.05$ using Kruskal-Wallis test across geographic region.

Fire history was difficult to determine in BMWC because of the rarity of fire-scarred trees in the

whitebark pine zone. It appears stand-replacement wildfires killed most trees leaving few firescars on the landscape. However, an approximate fire history was determined from stand age structure and the few fire scars found. The estimated fire return interval for the entire study area was approximately 144 years with a minimum of 55 and a maximum of 304 years. This is comparable to Gabriel's (1976) findings for high elevation forests of the southern BMWC. Average stand age was approximately 228 years with the oldest stands exceeding 400 years.

Image Classification

Only one combination of the TM bands generated error rates lower than 50% for the cover type and forest decline classifications (Bands 1-7 in Table 2). Overall error rates and KHAT statistics (measure of overall agreement) (Congalton 1991) indicate no particular band combination generated a superior classification. Rather, the use of all TM bands resulted in the best classifications (Table 2). Classification success was not improved when the NDVI transformation was included in the band combinations. Principal Components Analysis (PCA) explained most of the variation (91%) in the seven TM bands into three component images that were included as new layers in the GIS (Layers A, B, C in Table 2). These layers were also included in the classification effort with limited success. The four new layers generated from Canonical Components Analysis (CCA) also yielded

TABLE 2. Overall classification accuracy of evaluated TM band combinations and transformations before filtering and smoothing.

TM Band Combinations	Cover Type Classification		Forest Decline Classification	
	Overall Accuracy (%)	KHAT Accuracy (%)	Overall Accuracy (%)	KHAT Accuracy
2,3,4,5	34.2	24.8	47.0	29.2
2,4,5,7	28.8	18.8	43.3	23.5
3,4,5,6	33.7	24.3	52.7	36.6
3,4,5,6,7	44.6	36.3	54.2	38.3
1,3,5,7, NDVI	27.6	17.6	47.2	29.6
3,4,5, NDVI	21.4	11.2	43.4	24.9
1,3,4,5,7	36.3	26.8	50.3	33.0
1,2,3,5,7	32.6	23.2	48.7	32.2
1,2,3,4,5,7	27.1	18.4	54.5	38.0
1,2,3,4,5,6,7	56.5	49.0	70.4	56.6
PCA - A,B,C*	28.0	17.7	45.0	21.8
CCA - A,B,C,D*	42.0	32.5	48.3	25.1

*A,B,C,D are transformations of TM bands 1-7

high error rates when used in cover type classification (Table 2). In general, TM bands 3,4,5 were useful in cover type classification while bands in the infrared and thermal regions (bands 4-7) were best for forest decline classification.

Fourteen cover types were spatially classified from all seven TM spectral bands and added as a layer in the BMWC GIS (Table 3). The northern portions of the BMWC (Middle Fork zone) seem to be dominated by subalpine fir (19% of landscape) while the southern portions (southern Continental Divide) are dominated by whitebark pine (64%). Topographical and vegetation characteristics summarized from the macroplot data are shown for all cover types in Table 4. The lack of data for some cover types in Table 4 is because the macroplot data for those types were taken by the National Forest personnel and detailed tree and fuel information were not recorded (Bain 1990). The error matrix for the final cover type classification shows 60% overall accuracy and 52% KHAT accuracy (Table 5).

The forest decline classification used TM bands 3 to 7 to predict extent of whitebark pine decline in the BMWC (Table 6). Forest decline was rated to three broad mortality classes of low, moderate and high based on the health of whitebark pine

and density of standing dead trees (Table 7). Results of the imagery classification seem to agree with the field results with the Swan Front and Middle Fork zones experiencing the greatest decline (26 and 24% in high decline class, respectively) (Table 6). The lowest levels of mortality appear to be along the Sawtooth Range and Southern Continental Divide where 82% and 78% of the forested area is in the low to moderate decline class. Classification accuracy averaged 78% overall with a 68% KHAT accuracy (Table 8).

The spatial extent of cover types by decline class is shown in Table 9. Whitebark pine dominated stands (cover types 1,3,5,6,7) comprise the majority of subalpine land area in the BMWC (56%). Nonforest cover types (shrubs, herbs, rocks) occupy about 28% of the analysis area. Only about 15% of this nonforested area is capable of supporting trees as estimated from the macroplot data collected by the Flathead National Forest personnel. Cover types where subalpine fir is dominant (types 2,4,8) have the highest proportion of their land area in the high decline class. The whitebark pine-lodgepole pine cover type and the high elevation cover types with alpine larch (cover types 5-8) have the greatest portion of land in the low decline class.

TABLE 3. Land area summary (hectares) of the classified cover type by four BMWC geographic zones. Numbers in parenthesis are the percent of cover type within that geographic zone.

Classified Cover Types		BMWc Geographic Zones								
		Sawtooth Range		Swan Front		S. Cont Divide		Middle Fork		
Num	Name	1		2		3		4		Totals
1	PIAL-ABLA-PIEN	17,816	(41)	30,386	(42)	65,980	(48)	22,747	(39)	136,929
2	ABLA-PIEN-PIAL	2,145	(5)	4,467	(6)	8,533	(6)	3,838	(7)	18,983
3	PIAL-PICO-ABLA	1,440	(3)	2,930	(4)	10,397	(8)	2,143	(4)	16,910
4	ABLA-PIAL-PICO	0	(0)	27	(>1)	26	(>1)	9	(>1)	62
5	PIAL-PICO	1,806	(4)	4,443	(6)	10,755	(8)	1,895	(3)	18,899
6	PIAL-LALY-ABLA	34	(>1)	25	(>1)	58	(>1)	109	(>1)	226
7	PIAL-LALY	97	(>1)	1,897	(3)	972	(1)	1,101	(2)	4,067
8	ABLA-PIAL-LALY	85	(>1)	253	(>1)	262	(>1)	139	(>1)	738
9	PICO-ABLA	319	(1)	799	(1)	1,451	(1)	928	(2)	3,497
10	ABLA-PIEN	1,656	(4)	5,881	(8)	3,434	(2)	6,956	(12)	17,927
11	PICO	406	(1)	1,398	(2)	4,539	(3)	453	(1)	6,796
12	Shrubs	3,014	(7)	8,634	(12)	8,057	(6)	8,677	(15)	28,382
13	Herbs	4,357	(10)	4,560	(6)	7,542	(6)	4,209	(7)	20,668
14	Rock, Soil	10,561	(24)	7,207	(10)	14,701	(11)	4,705	(8)	37,174
Totals		43,735		72,907		136,706		57,909		311,257

TABLE 4. Ecological characteristics of classified cover types for the BMWC subalpine landscape. These values are computed as a mean across all macroplots within a sampled cover type.

Characteristic	Cover Type Number ²													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Cover type name ¹														
Dominant species	PIAL	ABLA	PIAL	ABLA	PIAL	PIAL	PIAL	ABLA	PICO	ABLA	PICO	SHRUB	HERB	ROCK
Secondary species	ABLA	PIEN	PICO	PIAL	PICO	LALY	LALY	PIAL	ABLA	PIEN				SOIL
Tertiary species	PIEN	PIAL	ABLA	PICO		ABLA		LALY						
Number Macroplots	50	31	14	2	9	2	2	2	5	50	5	50	50	50
Stand age (yr)	307	250	200	372	202	271	257	294	96	—	94	—	—	— ³
Whitebark pine—PIAL														
Cover (%)	30	17	19	11	28	20	25	10	1	2	1	4	2	0
Overstory age (yr)	257	229	199	284	209	171	175	286	—	—	—	—	—	—
Understory age (yr)	79	92	74	74	93	91	82	48	—	—	—	—	—	—
Understory density (trees/ha)	300	160	138	7	91	3	35	15	—	—	—	—	—	—
Standing Dead														
Basal area (m2/ha)	9.18	9.48	5.46	17.6	3.70	6.66	1.12	5.16	—	—	—	—	—	—
Density (trees/ha)	180	185	163	321	106	49	12	99	—	—	—	—	—	—
Rust severity														
Percent infection	82.1	87.6	84.9	70.8	79.0	79.0	50.0	100.0	—	—	—	—	—	—
Cankers/tree	10-15	15-20	10-15	10-15	10-15	5-10	10-15	10-15	—	—	—	—	—	—
Rust crown kill (%)	27.1	35.2	40.2	29.8	36.6	11.9	19.5	34.2	—	—	—	—	—	—
Subalpine fir—ABLA														
Cover (%)	17	26	13	30	5	20	6	15	10	30	1	8	3	0
Overstory age (yr)	170	157	96	159	135	240	101	—	—	—	—	—	—	—
Understory age (yr)	120	106	107	85	79	67	78	114	—	—	—	—	—	—
Understory density (trees/ha)	1960	1185	286	145	20	49	74	72	—	—	—	—	—	—
Engelmann spruce—PIEN														
Cover (%)	10	20	8	7	2	0	0	3	10	1	1	1	3	2
Overstory age (yr)	220	236	204	314	136	—	249	—	—	—	—	—	—	—
Understory age (yr)	108	69	91	84	55	—	—	—	—	—	—	—	—	—
Understory density (trees/ha)	311	195	106	15	10	0	15	0	—	—	—	—	—	—
Lodgepole pine—PICO														
Cover (%)	1	2	22	11	16	0	0	0	54	3	60	5	2	0
Alpine larch—LALY														
Cover (%)	1	0	0	0	0	20	20	10	0	0	0	0	0	0
Rock Cover (%)	12	15	15	20	31	14	5	8	2	7	25	13	25	60
Shrub Cover (%)	60	52	70	45	46	60	75	75	52	57	40	53	11	—
Herbaceous cover (%)	47	52	28	32	30	60	41	40	26	65	17	68	74	—
Elevation (m)														
Minimum	1927	1963	1961	2061	2030	2400	2376	2300	1927	1944	1919	1944	1997	—
Maximum	2490	2417	2332	2128	2445	2400	2384	2395	1859	1853	1829	1856	1853	—
Mean	2190	2170	2110	2090	2240	2400	2380	2350	2037	2164	2018	2195	2225	—
General Aspect	SE-SW	SE-SW	SE-SW	NE-SE	SE-SW	SW-NW	NW-NE	NW-NE	SE-NW	NE-SW	NE-SW	NE-SW	NE-SW	—
Slope (%)	34	31	31	20	33	42	29	46	27	37	50	27	25	—
Woody Fuel (kg/m ²)														
0 to 1 cm dia	0.02	0.01	0.02	0.00	0.01	0.00	0.02	0.00	—	—	—	—	—	—
1 to 3 cm dia	0.11	0.06	0.01	0.22	0.22	0.22	0.25	0.18	—	—	—	—	—	—
3 to 7.6 cm dia	0.36	0.29	0.25	0.22	0.22	0.22	0.25	0.63	—	—	—	—	—	—
7.6+ cm dia	3.23	2.06	1.34	1.34	2.26	2.10	3.60	2.22	—	—	—	—	—	—

¹PIAL—*Pinus albicaulis*, ABLA—*Abies lasiocarpa*, PIEN—*Picea engelmannii*, PICO—*Pinus contorta*, LALY—*Larix lyallii*

²Cover types 1-8 are described by data gathered in this study, cover types 9-13 are described by historical macroplot data gathered by the Flathead National Forest, cover type 14 (Rock) was described from photos.

³The symbol '—' denotes no data were available to compute average values

⁴SW—Southwest, SE—Southeast, NW—Northwest, NE—Northeast

TABLE 5. Error matrix comparing the agreement between ground truth pixels and the BMWC cover type classification. Overall accuracy was 60.1% and the KHAT accuracy was 51.9%.

Reference Cover Types	Classified Cover Types															Commission ¹ Error (%)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Tot	
1	398	28	14	0	4	0	9	0	0	22	2	77	54	14	622	37
2	122	153	11	0	0	0	0	0	1	53	0	36	26	0	402	62
3	19	5	60	0	5	0	5	0	2	3	9	17	0	0	125	52
4	9	0	0	5	0	0	0	0	0	0	0	13	0	0	27	82
5	2	0	0	0	68	0	0	0	0	0	0	2	0	0	72	6
6	10	0	0	0	0	4	15	0	0	1	0	14	1	0	45	92
7	0	0	0	0	0	0	14	0	0	0	0	0	0	0	14	0
8	18	0	0	0	0	0	0	18	0	0	0	0	0	0	36	50
9	8	0	10	0	0	0	0	0	18	0	0	0	0	0	36	50
10	30	0	0	0	0	0	0	0	0	45	5	27	9	0	116	62
11	1	7	0	0	0	0	0	0	0	0	27	0	0	0	35	23
12	26	14	0	4	34	0	1	0	0	0	0	99	17	9	204	52
13	32	2	0	0	15	0	0	0	0	0	0	40	126	41	256	51
14	22	0	0	0	13	0	0	1	0	3	0	0	10	418	478	11
Total	697	209	95	9	139	4	44	19	21	127	43	325	243	482	2457	40

Omission¹
Error 43 27 37 45 52 0 69 6 15 65 38 70 49 14 40

¹Commission error is the error of misclassifying a reference stand and Omission error is the error of not classifying the cover type correctly.

TABLE 6. Land area summary of classified forest decline classes for the cover types containing whitebark pine by the four BMWC geographic zones. Numbers in parenthesis indicate the proportion of the decline class within that geographic zone.

Classified Decline Class		BMWC Geographic Zones								Totals	
		Sawtooth Range		Swan Front		South Cont Div		Middle Fork			
1	Low	8,822	(38)	18,309	(41)	36,899	(38)	11,652	(36)	75,682	(39)
2	Moderate	10,323	(44)	14,802	(33)	39,152	(40)	12,799	(40)	77,076	(39)
3	High	4,277	(18)	11,317	(26)	20,932	(22)	7,530	(24)	44,056	(22)
Totals		23,422	(12)	44,428	(22)	96,983	(50)	31,981	(16)	196,814	

TABLE 7. Forest decline characteristics for BMWC whitebark pine stands.

Stand Characteristic	Forest Decline Class		
	Low	Moderate	High
Trees infected with rust	0 to 50%	51% to 90%	91% to 100%
Crown foliage killed	0 to 10%	11% to 40%	41% to 100%
Snag density (trees/ha)	0 to 10	10 to 50	>50

TABLE 8. Error matrix contrasting the agreement between ground truth pixels and the forest decline classification. Overall accuracy was 78.4% and KHAT accuracy was 67.8%.

Reference Decline Class	Classified Decline Class			Totals	Commission Error (%)
	Low	Mod	High		
Low	177	19	13	209	16
Mod	27	167	53	247	33
High	24	7	176	207	15
Totals	228	193	242	663	22
Omission Error (%)	23	14	28	22	

TABLE 9. Land area in hectares by classified cover type and forest decline class for the BMWC analysis area. Percent of forest decline class within a cover type are provided in parenthesis. Some cover types (9-14) did not have significant amounts of whitebark pine so no estimate by forest decline class was needed. Snow, ice and water were excluded from the analysis area.

Cover Type		Forest Decline Class				Total Land Area	
Num	Name	Low		Moderate		High	hectares %
1	PIAL-ABLA-PIEN	49,030	(36)	60,491	(44)	27,408 (20)	136,929 44
2	ABLA-PIEN-PIAL	5,584	(30)	5,342	(28)	7,804 (42)	18,983 6
3	PIAL-PICO-ABLA	3,246	(19)	9,526	(56)	4,138 (25)	16,910 5
4	ABLA-PIAL-PICO	7	(12)	1	(1)	54 (87)	62 >1
5	PIAL-PICO	13,083	(69)	1,626	(9)	4,190 (22)	18,899 6
6	PIAL-LALY-ABLA	217	(96)	7	(3)	2 (1)	226 >1
7	PIAL-LALY	3,994	(98)	71	(2)	2 (0)	4,067 1
8	ABLA-PIAL-LALY	521	(70)	12	(2)	207 (28)	738 >1
9	PICO-ABLA	0	0	0	0	0	3,497 1
10	ABLA-PIEN	0	0	0	0	0	17,927 6
11	PICO	0	0	0	0	0	6,796 2
12	Shrubs	0	0	0	0	0	28,382 9
13	Herbs	0	0	0	0	0	20,668 7
14	Rock, Soil	0	0	0	0	0	37,174 12
Totals		75,676	(39)	77,080	(39)	44,058 (22)	31,125 100

Discussion

Status of Whitebark Pine

Whitebark pine is rapidly declining in the BMWC, and the obvious causes are blister rust and successional replacement. There are very few areas in the BMWC where rust has not infected whitebark pine trees. It appears the rust epidemic is extensive with the majority of the forested analysis area (61%) in the moderate and high decline class (Table 9). A 1991-92 remeasurement of whitebark pine trees in historical plots located around western Montana first measured in 1971 indicate that approximately 2% of the species' basal area and

3% of its trees are lost each year (Keane and Arno 1993). At this rate it is estimated that most BMWC whitebark pine stands will move from the moderate to high decline class within about a decade. There is ample evidence from macroplot data that whitebark pine had been experiencing mortality for some time. There are many standing and fallen dead whitebark pine trees at most sites (Table 4) and it is estimated that most of these trees were killed by the rust.

It appears that the whitebark cone crop in the BMWC has greatly decreased. Field results show that about a third of all whitebark pine crowns are

now dead. Blister rust typically begins killing a tree by infecting and girdling the top of the crown, then spreading downwards on the trunk and eventually girdling the entire tree. Nearly all whitebark pine cones are produced in the upper third of the crown that is killed first by the rust. With 83% of whitebark pine trees infected and 61% of the analysis area in the moderate or high decline class, it seems the potential for the large cone crops that were historically common in BMWC subalpine forests (Cheff 1984) has been greatly reduced.

Historical stand structure and composition estimated from the macroplot data indicate that the majority of BMWC subalpine forests were, until recently, dominated by whitebark pine with a small component of subalpine fir and spruce in the overstory (Keane and Morgan 1994). Presence of an older age class of whitebark pine and the preponderance of whitebark pine snags indicate that these stands once supported about 20-30 m²/ha⁻¹ of whitebark pine and very little subalpine fir. Now, subalpine fir is abundant in both the understory and overstory because of this rapid mortality in whitebark pine (Table 4). This is evident from TM classification results considering cover types dominated by subalpine fir (cover types 2,4,8) have the highest proportion of their land area in the high decline class because blister rust-caused mortality of whitebark pine is accelerating succession to subalpine fir. In addition, approximately 14% of the forested BMWC subalpine landscape is dominated by fir and spruce (cover types 2,4,8,10 in Table 9). This seems higher than historical percentages considering the mean pre-1900 fire return interval (144 years estimated from this study) is less than the time it takes for subalpine fir to become dominant in the overstory (150 to 250 years estimated from data used in Table 4). Moreover, Ayres' (1901) estimate of 20 to 40% land area burned every 40 years would indicate that only a small portion of the BMWC landscape would be greater than 150 years old.

The exclusion of most fires on these landscapes over the last 60 years has also possibly contributed to a marked increase of subalpine fir both in the understory (PIAL-ABLA-PIEN cover type 1) and overstory (ABLA dominated cover types 2,4,8,10) (Table 4). This agrees with Arno (1986) and Kendall and Arno (1990) that whitebark pine is being successional replaced by the more shade-tolerant fir and spruce. Arno *et al.* (1993) found 14% of

their study area in the Bitterroot Mountains of Montana was dominated by whitebark pine in the early 1900's and none of that area was dominated by whitebark pine in 1991. Without fire, the shade-intolerant whitebark pine has limited success regenerating under closed canopies. The lack of whitebark pine regeneration in the sampled stands (Table 4) again suggests that the species will eventually be replaced by subalpine fir and spruce in the absence of fire.

This field study and Ayres' (1901) survey indicate that fires were important on the BMWC subalpine landscape. Fires that started during non-extreme weather years in the southern BMWC were rarely large and usually consumed scattered surface fuels (Arno 1986, Gabriel 1976). However, these surface fires tended to kill the fire-intolerant fir, spruce and young whitebark, but larger whitebark pine trees survived. This type of fire regime, although rare in the BMWC, maintained open, park-like stands of nearly pure whitebark pine (Arno 1986). Some stands of cover type 1 (PIAL-ABLA-PIEN) closely resemble this historical stand character except for the high coverage of fir and spruce which is perhaps linked to rust mortality and fire exclusion (Table 4). Extensive, stand-replacement fires such as those documented by Ayres (1901) and Losensky (1990) created burned areas heavily colonized by whitebark pine regeneration from nutcracker-cached seed. These large fires were probably a result of extreme dry, windy weather conditions and prolonged drought (Losensky 1990).

Blister rust severity seems to be related to geographic region within the BMWC. Results of both the field study (Table 1) and image classification (Table 6) indicate that whitebark pine mortality is higher in the northern and western portions of the wilderness. Stands near the Continental Divide in the southern BMWC tend to have less rust damage. This phenomenon may be related to climatic conditions during rust spore transport from the alternate host *Ribes* spp. (currant and gooseberry shrubs) to whitebark pine during late summer and early fall. Successful spore germination and infection requires warm, moist environments (Bingham 1972). Although these conditions occur infrequently in high elevation areas, they are more frequent in the modified-maritime climates of the northern and western BMWC than the southern portion of the area (Keane and Morgan 1994).

Image Classification

Accurate classification of BMWC subalpine cover types proved to be quite difficult. Past fire history, heterogeneous stand structure, similarity of cover types and varying soil parent material confounded classification results. Field sampling did not adequately cover the full range of successional community types for all subalpine cover types. Moreover, most BMWC subalpine forests are quite open, averaging 20 to 40% tree canopy cover with the understory mostly composed of shrubs and herbs (Table 4). The LANDSAT TM scanner estimates average spectral reflectance across a 30 meter square pixel. Therefore, the spectral signal from the open forested BMWC subalpine cover types were often confused with the signal from shrub and herb communities (Table 4). The opposite was also true. A high similarity of tree species across cover types also served to weaken the classification. Distinctions between some cover types were subtle and these similar types may be merged in the future. Lastly, subalpine community composition differed across limestone and non-limestone substrates resulting in limited success in using topographic rules to predict cover types without a soil layer in the GIS.

Shadowing in the LANDSAT TM scene also reduced classification accuracy. The sun elevation angle of 44 degrees and azimuth of 140 degrees resulted in extensive shadow across this topographically complex area. Fortunately, shadowing was not as severe in the high elevation areas, but many steep, subalpine north slopes were in some shadow which influenced classification results.

Inaccurate historical ECODATA macroplot locations caused high classification error rates. Macroplots established for this study were accurately located to within 10-30 meters using GPS instruments. However, the historical macroplots established for other classification efforts used USGS topographic maps and aerial photos to estimate spatial coordinates (Bain 1990). These historical locations were sometimes off by 100-200 meters. The overall accuracy increased from 60 to 83% when only plots from this study were used to test cover type classification (Table 10). However, this study located plots only in cover types that contained whitebark pine.

The forest decline classes were designed to recognize broad assessments of the amount of dead and dying whitebark pine on the BMWC landscape. Since blister rust is the major cause of this mortality, it was assumed that these classes would be related to blister rust severity. However, there probably were other situations that would give the same decline classes. For example, we noticed, but did not sample, abundant subalpine fir mortality in some portions of the northern BMWC that were classified to the high forest decline class. This is a situation where the majority of mortality is from subalpine fir rather than whitebark pine. The Gates Park fire of 1988 in the northern Sun River drainage (Figure 1) killed nearly all subalpine trees within its boundaries. This area was classified to the high decline class because of the great amount of fire-killed trees, not because of high blister rust mortality.

TABLE 10. Error matrix using only ECODATA plots geographically located with GPS. Overall accuracy 83.5% and KHAT accuracy was 75.2%.

Reference Cover Type	Classified Cover Type								Totals	Commission Error (%)
	1	2	3	4	5	6	7	8		
1	323	16	7	0	1	0	0	0	347	7
2	61	111	6	0	0	0	0	0	178	38
3	6	5	58	0	5	0	5	0	79	27
4	0	0	0	5	0	0	0	0	5	0
5	2	0	0	0	68	0	0	0	70	3
6	5	0	0	0	0	4	0	0	9	56
7	0	0	0	0	0	0	14	0	14	0
8	0	0	0	0	0	0	0	18	18	0
Totals	397	132	71	5	74	4	19	18	720	17
Omission Error (%)	19	16	19	0	9	0	27	0	17	

Implications of Whitebark Pine Decline

The consequences of whitebark pine decline in the BMWC could be devastating for some animal and plant species. The BMWC is one of the few remaining ecosystems with substantial numbers of grizzly bears that historically depended on abundant whitebark pine cone crops (Craighead *et al.* 1982). As the cone crops dwindle, bears must either migrate or find a new source of prehibernation food-stuffs (Mattson *et al.* 1991, Kendall 1980). Squirrels and Clark's nutcrackers will also need to find alternate food sources, as will those animals that depend on them (Ferner 1974). Moreover, the Clark's nutcracker will tend to eat proportionally more seeds when the available seed supply is low (Tomback 1982). Therefore, whitebark regeneration potential will be somewhat reduced because fewer seeds will be cached and most of the seeds cached will probably be excavated. Shifts in vegetation composition and wildlife migration as whitebark pine declines can invoke major changes in the diversity and structure of the subalpine landscape.

An important step towards sustainable management of whitebark pine ecosystems is inventory. The extent and severity of whitebark pine decline is mostly unknown in the northwestern United States. Most western United States national parks have yet to identify the extent and condition of their whitebark pine forests (Kendall 1993). Very few high elevation forests are inventoried on national forests by the USDA Forest Service probably because they have little commercial value and are somewhat inaccessible. Identification of whitebark pine health and status on the regional landscape can provide important information for various projects such as rust-resistant breeding programs or grizzly bear relocation programs. It is also neces-

sary for developing strategies for restoring whitebark pine across its range.

Conclusions

Blister rust is killing many whitebark pine trees across the BMWC. The heaviest mortality is occurring in the modified-maritime climates of the northern and western portions of the BMWC. The potential for large whitebark pine cone crops has been severely reduced because the rust tends to kill the cone-bearing branches first. This will affect the many animals that utilize whitebark pine seed.

Successional replacement of whitebark pine by subalpine fir and Engelmann spruce is also a major cause of whitebark pine decline. Policies of fire exclusion in the BMWC over most of the last 50-60 years has resulted in a high proportion of subalpine forest area dominated by subalpine fir and spruce. Moreover, those areas currently dominated by whitebark pine have an abundance of subalpine fir in the understory. Lastly, the high rust-caused mortality in whitebark pine has accelerated succession to subalpine fir dominance.

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Book Review

Compass and Gyroscope: Integrating Science and Politics for the Environment.

Kai N. Lee. Island Press (\$24.95)

By its very name, the June 1992 United Nations Conference on Environment and Development in Rio de Janeiro focused attention on the concept of sustainable development. The term is generally defined as development that meets the needs of current generations without compromising the resource needs of future ones. The theme of the conference was to find solutions to what many perceive as the irreparable harm perpetrated by mankind upon the planet. To do that, conference participants acknowledged, may require a complete restructuring of society, especially as it relates to the global distribution of wealth, resources and technology.

The debate over sustainability is not a new one. It has, however, become more politicized in the past three decades, especially in the United States. The pivot point appears to be a questioning of the role of science in environmental policymaking. Should policy be made by officials who are openly partisan and parochial but also subject to the will of their constituency (the linchpin of a democratic society), or by scientists who are ideally more unbiased but totally unaccountable to the public?

Conservatives contend that many decisions about environmental policy have been made on the basis of political posturing, rather than on factual evidence gathered through impartial scientific investigation. They believe that what they perceive to be intrusive government policies are the result of scare tactics from environmental extremists and an unquestioning media, citing global warming and ozone depletion as examples of the misuse of science. Authors like Dixy Lee Ray, for example, believe that human stewardship of resources is not only possible but preferable to losing control of our own destiny to what she calls "environmental evangelists."

Liberals, on the other hand, believe that conservatives are less interested in science than in erecting barriers to obstruct and stall the policy process. They criticize the reticence of regulated businesses to comply with even basic environmental legislation as examples of why the command and

control approach is necessary. United States Vice President Al Gore argues that there is already sufficient scientific evidence that the global environment is rapidly deteriorating, and calls for immediate steps to be taken to save what remains of the planet's resources. Gore believes such an effort could be launched through a Global Marshall Plan in which the scientific and technological resources of the developed nations would be made available to Third and Fourth World countries.

Dr. Kai N. Lee, director of the Center for Environmental Studies at Williams College, attempts to satisfy both ends of the political spectrum in his book *Compass and Gyroscope: Integrating Science and Politics for the Environment*. He argues that there is a place for both science and politics at the policymaking table, with social learning as a means to achieve sustainable uses of the natural environment.

The author's "compass and gyroscope" title might better have been reversed with its subtitle, since it is difficult to follow the metaphor from one chapter to the next. The compass that Lee proposes is that natural resource policy should be based on adaptive management—a process he defines as learning from structured experimentation. He notes that adaptive management is different from trial and error experimentation because the concept relies on a carefully controlled process where hypotheses are tested and information diligently gathered so that mistakes are not repeated.

The gyroscope of Lee's model is the concept of bounded conflict—allowing for the diversity of opinion that is an integral element of a democratic society while still maintaining control through a commitment to continual debate. This combination of adaptive management and bounded conflict through political change are essential to what Lee terms social learning, an important component of sustainability in large ecosystems.

The model itself is introduced in the author's initial chapter, and then tested on the Columbia River Basin as a case study in sustainability. Lee's insight on this region is impressive; in 1983 he was appointed by the governor of Washington to serve as a member of the Northwest Power Planning Council. The Council produced two regional plans to guide future electric power development, based

largely on forecasts of economic and population growth. In addition, the project financed a \$20 million, three-year study of energy efficiency in Hood River, Oregon, described in some detail in his book.

He follows with a comparative analysis of the model using three other case studies of the rain forest in Queensland, Australia, forest practices in the Pacific Northwest, and a salmon enhancement project in Canada. The final chapters focus on his call for a new "civic science" to manage large ecosystems—a blending of idealistic science and pragmatic politics.

From a purely stylistic standpoint, Lee's writing is best when describing the Columbia Basin study. He obviously is writing about a project close to his heart, yet the language is objective and the explanations understandable. The rest of the book is written in a totally different voice, as if Lee was a poet rather than a political scientist. At times the prose is philosophical and almost pleading, plaintively asking why the participants in the debate can not just put aside their differences for a few moments to navigate a course agreeable to both sides.

Is Lee successful in convincing us that this model can be successfully applied to environmental policy? The answer depends largely on which end of the political spectrum the reader identifies with most.

Committed environmentalists are likely to be impatient with Dr. Lee's prescriptions. His fondness for lengthy and corroborated scientific exploration may be perceived as pandering to big business" calls for more research. Certainly, there is some merit to their concern, since Lee limits the application of his model to resource issues (timber and fisheries) rather than more complex ones like stratospheric ozone depletion and global

climate change. If the model were to be applied to those issues, it is likely that Lee would support continued evaluation and research rather than international agreements and regime formation.

Conservatives may infer that Lee champions a kinder and gentler form of policymaking more to their liking than that of the environmental movement. He does appear to support what he terms "environmental imperialism" as a win-win solution to sustainability. Lee would allow resource exploitation in poor countries, and the shifting of manufacturing to those regions to take advantage of their role as both potential consumers and as an untapped labor pool. He views this as a way of building the economy of developing nations while reducing two of the causes of domestic unrest in the developed world, immigration and pollution. But he also speaks to the issue of equity, pointing out the fact that today's developing countries are the inheritors of colonialism. Lee is not so much pro-progress and development as he is aware of the momentum of unsustainability that is a legacy of our history on the planet.

The author admits in both the preface and the prologue that this book is not an attempt to offer a solution to sustainability; in fact, he acknowledges in the final chapter that it is possible a solution does not even exist. But he does offer some hope that we will continue to strive towards it, much as we strive towards freedom or justice. He closes with a call for patience "in cultivating a world where we can all live together." Environmental leaders may simply not be willing to wait that long.

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Northwest Science

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Information for Authors—A complete copy of the *Northwest Science* "Information for Authors" is available from the Editor.

Page Charges—Page charges are currently \$60 per printed page. Petition for partial payment or waiver of these charges should be directed to the Editor upon acceptance of a manuscript for publication.

Manuscripts—Submit four copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten on 8½ x 11 paper and *double-spaced throughout (including abstract, acknowledgments, literature cited, tables, and legends for figures)*; provide ample margins. Avoid unnecessary footnotes. Do not break words at the end of a line. Format and style of manuscripts should conform to general usage in recent issues.

An abstract, written in complete sentences and not exceeding 250 words, should precede every article. It should succinctly state the objectives, the experimental design, the principal observations, and conclusions of the paper. Authors are reminded of the diverse disciplines and readership served by the journal; with this in mind, the abstract should conclude with a sentence or two stating the broader significance of the paper.

Literature citations should have the author's name and year of publication in the text; e.g. (Jones 1978). Citations should be double-spaced and listed in alphabetical order at the end of the article.

Present all data in international (SI) units. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2300) and continental dating (17 November 1990).

Equations should be presented camera-ready. Symbols should be large enough to be legible after a ⅓ to ½ reduction in size, but not overly large.

Tables should be typewritten (double-spaced) separately from the text. Original art work or glossy prints of photographs must be submitted for reproduction. Art work and lettering should be large enough (but not overly large) to provide clarity after a 50 percent reduction in size for printing. The author's name and figure number should be penciled on the back of each illustration. Provide a scale for distance on map illustrations. Legends for illustrations should be typed (double-spaced) as a section of the manuscript; do not use a separate page for each legend.

Length of manuscripts is limited to 15 pages of printed copy. Two typed pages are approximately equal to one journal page. **The final versions of accepted manuscripts are requested to be submitted on 3 1/2" diskettes with appropriate file names and word processing software indicated.**

Authors of Biological Papers—On first mention, a species should be designated by common name followed by systematic binomial. For abbreviations and forms of titles for serial publications, follow the *BIOSIS List of Serials*. Consult with the *Council of Biology Editors (CBE) Style Manual*, 4th ed., for general information on manuscript preparation.

Correspondence—Correspondence will be between the designated corresponding author and the Editor.

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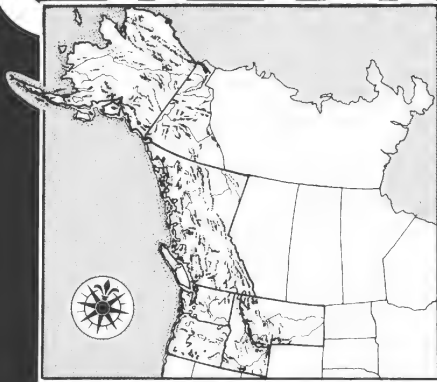
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November 1994

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DECLINE IN OREGON

NORTHWEST SCIENCE



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The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

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Announcements

Notice of Annual Meeting

The 68th Annual Meeting of the Northwest Scientific Association will occur jointly with the Idaho Chapter of the Wildlife Society on March 9-11, 1995. Registration will begin on the evening of March 8. The meeting, hosted by Idaho State University, will occur at the ISU/UI Center for Higher Education Facility and the Shilo Inn (Reservations: 1-800-222-2244) Idaho Falls, Idaho. Idaho Falls is located in the southeastern corner of the state along the Snake River. Famous for its falls, the city lies in the heart of some of the world's best known recreation areas, including Yellowstone and Grand Teton National Parks, Lava Hot Springs, Sun Valley, Henry's Lake, Craters of the Moon National Monument, the Sawtooths, Jackson Hole, and Salt Lake City, all within a three-hour drive from Idaho Falls. The city is served by Delta, Horizon and Skywest airlines.

G. Wayne Minshall, internationally recognized expert on stream ecosystem structure and function, and recipient of the NSA Outstanding Scientist Award in 1993, will be the guest speaker at the Thursday evening banquet.

NSA symposia:

■ *Ecological Aspects of Waste Management*—Thursday morning

- Purpose of waste isolation: Legal requirements and design criteria
- Existing low-level waste repositories
- Challenges to waste repositories: Animal intrusion
- Challenges to waste repositories: Paleoclimate
- Challenges to waste repositories: Plants and water
- Meeting the challenges: Engineered designs
- Meeting the challenges: Ecological solutions

■ *Distance Education: The New Frontier*—Friday afternoon

- Programs in other states
- What is new in educational technology—hardware vs. software
- Overcoming the challenges

■ *Geology of the eastern Snake River Plain*—Friday morning

- Seismotectonics of the Snake River Plain—Yellowstone region
- Upper crustal seismic and geologic structure of the ESRP
- Upper mantle structure along the Snake River plain
- Overview of eastern Snake River plain volcanic geology
- Genesis of rhyolite domes and flows of the ESRP
- Tuffs of Trapper Creek, Idaho
- Loess distribution and sources of southeastern Idaho
- Use of radioisotopic tracers to refine the conceptual model of ground-water movement

Sectional papers in Mathematics, Geology/Geography, Chemistry, Physics, Zoology, Botany, and Forestry are planned.

For information about presenting papers contact: Dr. Barry Keller, 208-236-3207.

Abstract submission deadline is February 1, 1995.

1995 Student Research Grant

I. ELIGIBILITY—Applicants must be regular members of the Northwest Scientific Association. *Northwest Science* (the journal of the society) has information for joining the society.

II. PREPARATION OF THE PROPOSAL—A cover page should be provided to include: Name and address of applicant, associated institution, name of major professor/advisor, degree program, year in school, and amount of money requested (maximum of \$500).

The proposal should include: Title, Statement of Justification, Methodology/Experimental Design (including methods of analysis), and detailed budget (on separate page).

The proposal length should be no more than three (3) *double spaced* pages (not including budget page).

Proposals are due on or before February 7, 1995 and should be sent to: Dr. R. Gerald Wright, Dept. Fish & Wildlife Resources, University of Idaho, Moscow, ID 83844-1136; phone: 208-885-7990.

Grants will be awarded at the annual meeting of the Northwest Scientific Association held in Idaho Falls, Idaho, March 8-11, 1995.

Awards provided by the Northwest Scientific Association are designed to help students complete research projects in the basic and applied sciences and social sciences. Monies should be used only to support research activities of the student. It is expected that students will report results of their research at a future NSA meeting.

Forest Health Decline in Central Oregon: A 13-Year Case Study

Abstract

A 200-ha mixed-conifer forest in central Oregon was examined in 1979 and 1992 to document causes of forest health decline. Between 1979 and 1992, grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) saplings increased significantly in stems/ha. In 1979, grand fir experienced the most mortality which was caused primarily by the root pathogen, *Armillaria ostoyae* (Romagn.) Herink and the fir engraver (*Scolytus ventralis* LeConte). In 1992, grand fir again experienced the highest mortality caused by root diseases and associated bark beetles. Additional mortality, primarily of grand fir seedlings and saplings, was associated with western spruce budworm (*Choristoneura occidentalis* Freeman). Eventually, a complex of pest species should reduce fir abundance, and surviving trees will benefit from the pest-altered tree biomass recycled as nutrients if catastrophic wildfires do not occur first. Forest health will continue to decline as grand fir and other fir species increase. Traditional silviculture and its new modifications can improve forest health if pest populations are recognized and less susceptible tree species are increased.

Introduction

Forest health can be simply defined as the condition of a forest, but to define a healthy forest is much more difficult. Abstract concepts such as resistance and resilience to disturbances, biological diversity, and sustainable productivity, all similarly difficult to define, are often linked to the concept of a healthy forest. Also, a healthy forest is often perceived in terms of management objectives or desired future condition.

Many areas in northeastern and central Oregon have recently experienced an apparent rapid deterioration of forest health (Figure 1). Forest health decline is manifested by dead foliage, crowns, and entire stems at landscape levels. Causes are long-term and complex. Fire exclusion and selective harvesting beginning at the turn of the century have resulted in an unprecedented abundance of grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in many areas. Many areas are overstocked with firs, resulting in excessive moisture stress for all trees on the site. Firs are prime hosts for many pests, including several species of defoliating insects, root diseases, and bark beetles. Severe defoliation by the western spruce budworm (*Choristoneura occidentalis* Freeman) has occurred for more than 10 years. Tree mortality has been accentuated by bark beetles, root diseases, and prolonged drought. Apparent lack of regulation of pest populations by natural enemies such as birds, ants, and spiders is being investigated (Torgersen *et al.* 1990).

Salvage logging is seen by many as a current panacea to the problem, but the harvesting of liv-

ing but root-diseased trees has contributed to the forest's poor health (Filip and Goheen 1982, Hagle and Goheen 1988). Clearcutting can decrease the abundance of fir and the frequency of pests, but because of public concern, the amount of clearcutting will decrease on public and perhaps private lands.

As typical for many areas in the interior West, the study area in central Oregon has a history of selective harvesting of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.). From 1917 to 1930, a period of subnormal precipitation occurred, resulting in widespread attack of ponderosa pine by the western pine beetle (*Dendroctonus brevicornis* LeConte) (Miller and Keen 1960). Salvage of dead trees was accelerated, but living pines with poor crown form and size were also harvested in anticipation of beetle-caused mortality. Many of these trees, however, were also infected with the root pathogens *Armillaria ostoyae* (Romagn.) Herink, *Heterobasidion annosum* (Fr.) Bref., and *Lep-tographium wagenieri* var. *ponderosum* (Harrington and Cobb) Harrington and Cobb, which cause crown decline before actual tree death. Harvesting living but root-infected trees exacerbated infection and mortality of the adjacent trees, especially the highly susceptible true firs (*Abies* spp.) that were present in the understory (Filip and Goheen 1982).

The causes of forest health decline in the Pacific Northwest are often debated, but quantification of such changes and causes is rarely reported. This paper presents evidence of forest health decline and its causes in mixed conifers from 1979 to 1992.

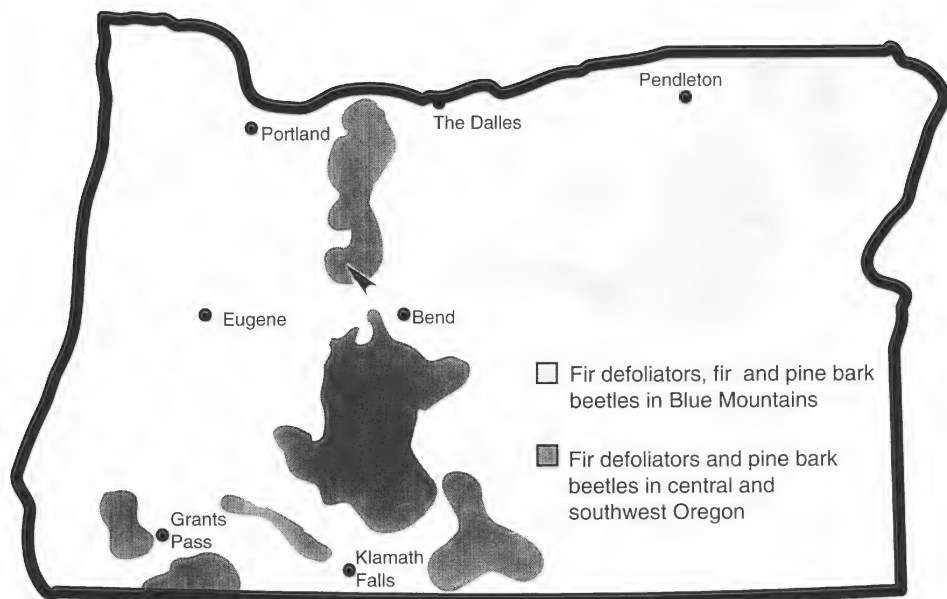


Figure 1. Recent forest pest-caused damage in eastern and southern Oregon with location (arrow) of the 200-ha study area.

Methods

In 1979 and 1992, a 200-ha area about 16 km NW of Sisters, OR (Figure 1) was examined. The site was on the Deschutes National Forest, with a mean elevation of about 1280 m and a site index of 24–27 m at 100 years. Currently, grand fir, white fir (*A. concolor* (Gord. and Glend.) Lindl. ex Hildebr.), and ponderosa pine dominate, with lesser amounts of lodgepole pine (*P. contorta* Dougl. ex Loud.), noble fir (*A. procera* Rehd.), Pacific silver fir (*A. amabilis* Dougl. ex Forbes), and subalpine fir (*A. lasiocarpa* (Hook.) Nutt). Several plant associations are present, varying with aspect and elevation, but grand or white fir is always climax. In 1983 and 1985, six 2.4- to 9.7-ha units (56.7 ha total) within the study area were either clearcut or shelterwood harvested; during 1986 to 1989 they were planted with mostly ponderosa pine. The shelterwood was a mixture of fir and pine.

The area was surveyed in 1979 and in 1992 by following six transects spaced at 200-m intervals. Plots were located every 200 m along the transects. Because permanent plots were not initially established, the exact plots measured in 1979 could not be remeasured in 1992. Permanent plots

were established in 1992 to monitor future tree growth and mortality. In 1979 and 1992, 57 variable-radius plots were used to estimate basal area and stems/ha for trees with diameters ≥ 12.7 cm at 1.4 m above ground (dbh). At each plot center, trees were tallied with a prism (basal area factor 4.6 m²/ha). Trees < 12.7 cm dbh but ≥ 15.2 cm in height were tallied on 57 fixed-area (0.004 ha) circular plots in order to determine stems/ha (only) for seedlings and saplings. Variable-radius plots and fixed-area plots had the same centers.

Data recorded for each plot tree included: (1) species, (2) dbh, (3) tree condition (live, dead), and (4) if dead, cause of mortality. Data for grand fir and white fir were combined because these species often hybridize and are difficult to distinguish, especially when defoliated. Data for noble fir, Pacific silver fir, and subalpine fir were combined because these species also are difficult to distinguish when defoliated.

The 1979 and 1992 surveys were done primarily to quantify damage caused by root diseases and associated bark beetles (Filip and Goheen 1982). Only dead trees or living trees with aboveground symptoms were examined for pathogens or bark beetles. Because such trees are often short-lived,

data for living but infected trees were combined with data for dead infected trees. Estimates of root-infected trees thus do not include living infected trees without aboveground symptoms. Root diseases were detected by limited excavation and dissection of major roots near the root collar. Bark beetles were identified by observing subcortical insect galleries. In order to avoid confusing trees killed before 1979 with those killed later, the 1992 tally of dead trees included only those trees killed during the last 10 years, as determined by bark condition.

Significant ($P \leq 0.05$) differences in tree species frequencies and mortality agents between survey years were determined by a t-test.

Results

Despite harvesting and mortality in the 200-ha area, live-tree basal area and trees/ha increased from 1979 to 1992 (Tables 1-4, Figure 2). Grand fir saplings (dbh = 2.5 to 12.4 cm) increased significantly in stems/ha between 1979 and 1992 (Table 1, Figure 2C). Increases in fir have occurred both outside and inside the harvested units, despite the fact that only pine was planted. There was

much variability among plots in stem frequencies, which probably accounted for the lack of statistical significance between survey years in all means except grand fir saplings/ha.

Defoliation by western spruce budworm was not detected in 1979. In 1992, however, it was present to some extent on every fir tree examined. Because defoliation of new foliage had been occurring every year since 1985, many trees, especially seedlings or saplings, which have a larger proportion of new foliage than mature trees, were completely defoliated yet still living. Also, because the roots of symptomless trees were not examined, the true number of trees with root infections is unknown; based on studies in other areas (Filip 1986), the true number may be at least twice the number of trees showing root disease symptoms.

Mortality caused by root diseases, primarily *Armillaria ostoyae* and *Heterobasidion annosum* in true fir saplings has generally increased, although not significantly, in 13 years (Table 1, Figure 3). Bark beetles associated with root disease include primarily the fir engraver (*Scolytus ventralis* LeConte) on grand fir. Mortality from causes other than root disease and associated bark beetles, mostly western spruce budworm, increased,

TABLE 1. Changes in basal area and density of *grand fir* and mortality agents from 1979 to 1992 on a 200-ha site in central Oregon.

	Living		Dead-Root Disease		Dead-Other Causes	
Year	Mean	Std. dev.	Mean	Std. dev.	Mean	Std. dev.
-----Basal area (m ²)/ha-----						
1979	8.7	23.0	0.6	1.9	0.1	0.6
1992	14.6	17.8	0.8	2.0	0.3	1.2
Z-value ¹	1.218ns		0.557ns		1.567ns	
-----Trees (>12.7cm DBH)/ha-----						
1979	103.9	280.9	10.6	41.9	1.4	11.9
1992	202.7	358.3	5.5	16.8	3.3	15.2
Z-value	1.414ns		1.249ns		0.850ns	
-----Saplings (2.5-12.7cm DBH)/ha-----						
1979	82.3	239.8	5.4	36.2	1.8	21.1
1992	299.0	608.1	34.7	118.4	26.0	120.7
Z-value	2.364*		1.835ns		1.505ns	
-----Seedlings (<2.5cm DBH)/ha-----						
1979	699.8	2142.7	3.6	36.4	1.8	21.1
1992	1209.0	1880.3	4.3	32.7	30.3	175.1
Z-value	1.098ns		0.133ns		1.226n	

¹ Z-value for t-test. * = means between years are significantly ($P \leq 0.05$) different; ns = non-significant.

TABLE 2. Changes in basal area and density of *other true fir species* and mortality agents from 1979 to 1992 on a 200-ha site in central Oregon.

	Living		Dead-Root Disease		Dead-Other Causes	
Year	Mean	Std. dev.	Mean	Std. dev.	Mean	Std. dev.
-----Basal area (m ²)/ha-----						
1979	1.2	5.3	0.3	1.5	0	0.3
1992	2.9	4.4	0.4	1.6	0.2	1.0
Z-value ¹	1.485ns		0.631ns		1.618ns	
-----Trees (≥ 12.7cm DBH)/ha-----						
1979	22.9	95.1	4.0	26.2	0.3	5.0
1992	53.2	93.4	5.1	19.3	3.5	17.3
Z-value	1.421ns		0.330ns		1.373ns	
-----Saplings (2.5-12.7cm DBH)/ha-----						
1979	49.4	198.9	0.9	14.9	0	0
1992	73.7	218.8	0	0	0	0
Z-value	0.523ns		0.739ns		-	
-----Seedlings (< 2.5cm DBH)/ha-----						
1979	16.5	73.0	0	0	0.9	14.9
1992	56.3	203.6	0	0	0	0
Z-value	1.323ns		—		0.739ns	

¹ Z-value for t-test, ns = means between years are not significantly ($P \leq 0.05$) different.

TABLE 3. Changes in basal area and density of *ponderosa pine* and mortality agents from 1979 to 1992 on a 200-ha site in central Oregon.

	Living		Dead-Root Disease		Dead-Other Causes	
Year	Mean	Std. dev.	Mean	Std. dev.	Mean	Std. dev.
-----Basal area (m ²)/ha-----						
1979	11.5	28.2	0.7	2.7	0.1	0.8
1992	12.3	14.2	0.4	1.3	0.2	1.0
Z-value ¹	0.155ns		1.125ns		0.932ns	
-----Trees (≥ 12.7cm DBH)/ha-----						
1979	56.4	164.4	5.8	31.1	0.6	5.1
1992	66.5	173.1	1.7	6.6	0.4	1.7
Z-value	0.267ns		1.528ns		0.421ns	
-----Saplings (2.5-12.7cm DBH)/ha-----						
1979	90.6	397.6	3.6	36.4	0.9	14.9
1992	95.2	254.6	0	0	0	0
Z-value	0.006ns		0.059ns		0.739ns	
-----Seedlings (< 2.5cm DBH)/ha-----						
1979	148.2	496.5	1.8	21.1	3.2	47.1
1992	182.0	474.9	0	0	30.3	229.0
Z-value	0.306ns		1.047ns		0.873ns	

¹ Z-value for t-test, ns = means between years are not significantly ($P \leq 0.05$) different.

TABLE 4. Changes in basal area and density of *lodgepole pine* and mortality agents from 1979 to 1992 on a 200-ha site in central Oregon.

	Living		Dead-Root Disease		Dead-Other Causes	
Year	Mean	Std. dev.	Mean	Std. dev.	Mean	Std. dev.
-----Basal area (m ²)/ha-----						
1979	1.5	4.5	0.1	0.6	0	0.3
1992	1.6	3.6	0	0	0.1	0.6
Z-value ¹	0.086ns		1.667ns		0.764ns	
-----Trees (≥ 12.7cm DBH)/ha-----						
1979	17.0	50.9	0.9	7.2	0.1	2.1
1992	39.5	104.9	0	0	0.8	6.1
Z-value	1.346ns		1.524ns		0.844ns	
-----Saplings (2.5-12.7cm DBH)/ha-----						
1979	8.2	48.8	0	0	0	0
1992	13.0	55.6	0	0	0	0
Z-value	0.415ns		—		—	
-----Seedlings (< 2.5cm DBH)/ha-----						
1979	164.7	545.3	1.8	29.8	3.6	59.7
1992	47.7	157.9	0	0	0	0
Z-value	1.150ns		0.739ns		0.739ns	

¹ Z-value for t-test, ns = means between years are not significantly ($P \leq 0.05$) different.

although not significantly, in the fir seedlings and saplings. However, grand fir mortality attributed to root disease and associated bark beetles in 1992 was often associated with defoliation by western spruce budworm. Hence, cause of mortality was difficult to assign to one pest species, and associations between *Armillaria ostoyae* and western spruce budworm in grand fir seedlings are being investigated (Parks 1993).

Discussion

In many ways, the 200-ha area that was surveyed in 1979 and 1992 is similar to many mixed-conifer ecosystems in the interior West, where climax species such as grand fir or other true firs continue to become dominant over such seral species as ponderosa pine. In 1979, most of the mortality in the study area could be attributed to root diseases and associated bark beetles. Other diseases such as fir dwarf mistletoe (Filip 1984) and stem decays (Aho *et al.* 1987) continue to contribute to the decline of forest health.

Despite harvesting and pest-caused fir mortality in unharvested areas, the amount of fir increased between 1979 and 1992; at the same

time, pests such as the western spruce budworm became more evident. By 1992, much of the additional mortality in the study area could be attributed to budworm, especially in fir saplings and seedlings. Most of the living but defoliated seedlings and saplings can be expected to die within a year, and many of the larger defoliated trees will be attacked by fir engravers and die. Likewise, living trees with advanced symptoms of root disease will probably be attacked by fir engravers and die within a year.

The mixed-conifer ecosystem will, in time, temporarily stabilize. A complex of pest species should reduce the stocking and basal area of firs through repeated defoliation, root and stem infections, and subsequent tree mortality; simultaneously, surviving trees will benefit from insect frass, needle drop, and woody debris recycled as nutrients. Tree mortality will eventually reduce intertree competition for space and moisture. However, there is a high probability that this entire process may be interrupted because of catastrophic wildfire as a result of accumulated woody debris, dead canopy fuels, and extended periods of drought.

In potted seedling studies, defoliation during drought also reduces transpiration in firs and thus

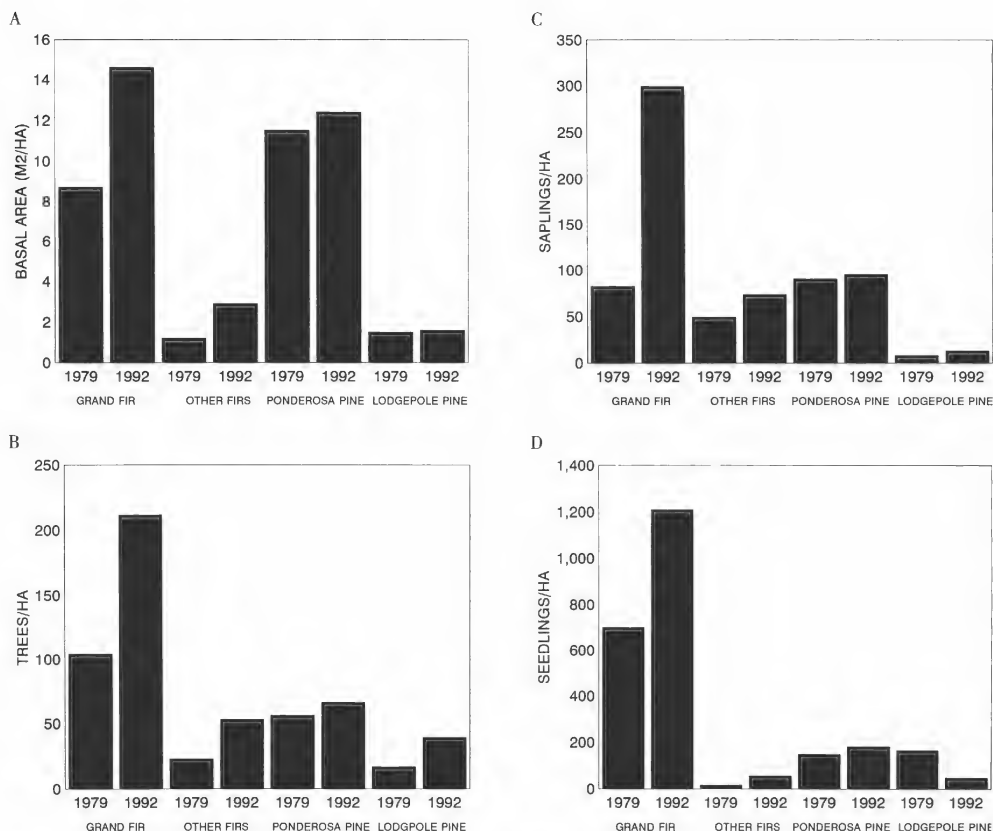


Figure 2. Changes in frequency of tree species (living trees only) from 1979 to 1992 on a 200-ha site in central Oregon: (A) Basal area/ha of stems ≥ 12.7 cm dbh, (B) Trees/ha (≥ 12.7 cm dbh), (C) Saplings/ha (2.5 to 12.7 cm dbh), and (D) Seedlings/ha (< 2.5 cm dbh). Live trees include living but defoliated and/or non-symptomatic root-infected trees.

uptake of nutrients and water (Parks 1993). Water and nutrients should thus become available for use by adjacent undefoliated tree species that are perhaps better adapted to periodic drought conditions; pines growing in association with firs have been shown to increase growth as a result of repeated defoliation of the fir (Carlson *et al.* 1985, Filip and Parks 1987).

Much of the tree mortality observed in 1979 was attributed to the chronic salvage program, which resulted in exacerbated infection by root pathogens and associated bark beetle attack (Filip and Goheen 1982). Living trees have defense mechanisms that prevent root pathogens from advancing along root systems to the root collar, which results in tree mortality. Dead trees lack these de-

fense mechanisms, and root pathogens quickly spread throughout the entire root system after infected trees are killed or harvested. This causes an increase in inoculum potential and mortality of adjacent living trees. In many areas in the interior West, repeated stand entries aimed at partial removal of dominant dead and dying trees have led to increased mortality of residual trees by root diseases and associated bark beetles (Shaw *et al.* 1976, Filip 1977, Hagle and Goheen 1988, Schmitt *et al.* 1991). Salvage of dead and dying trees recovers wood that would normally be lost, but if proper silvicultural techniques are not used to convert stands to less pest-prone species, residual trees will continue to be attacked and killed (Oester *et al.* 1992). Recent efforts to accelerate

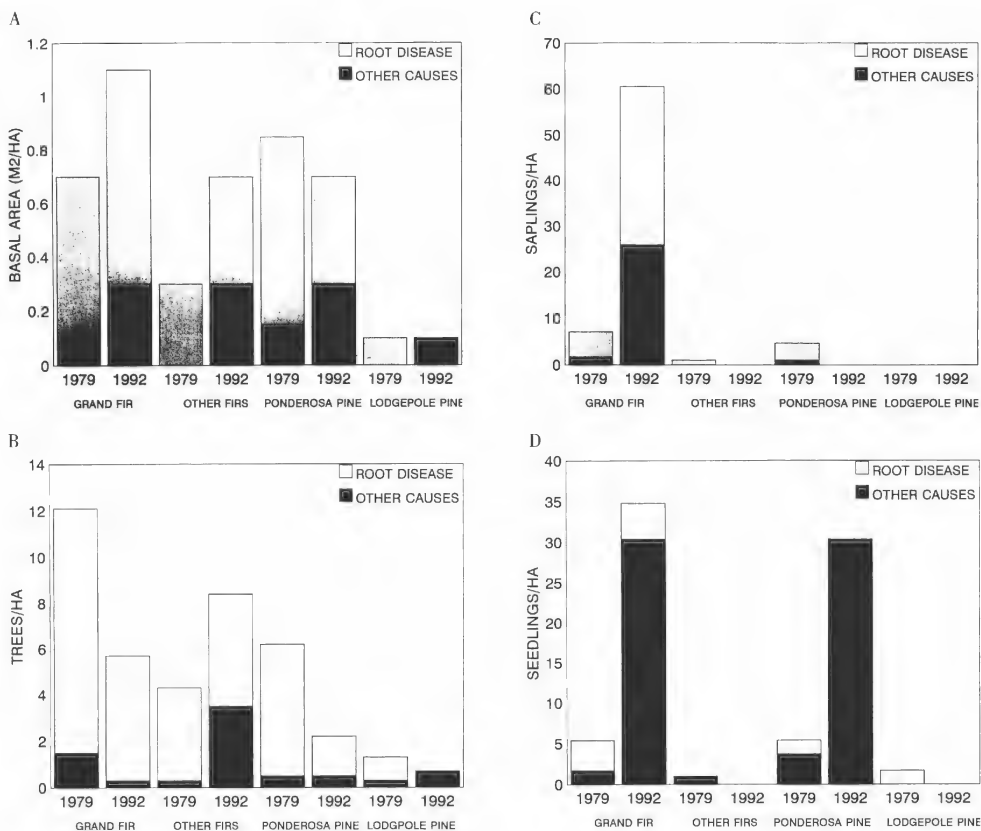


Figure 3. Changes in frequency of tree species (dead trees only) from 1979 to 1992 on a 200-ha site in central Oregon: (A) Basal area/ha of stems ≥ 12.7 cm dbh, (B) Trees/ha (≥ 12.7 cm dbh), (C) Saplings/ha (2.5 to 12.7 cm dbh), and (D) Seedlings/ha (< 2.5 cm dbh). Root diseased trees include dead trees and living trees (symptomatic) with severe root collar infections.

salvage programs in areas experiencing poor forest health, such as those in northeastern Oregon, may only accentuate long-term forest decline by increasing existing root disease areas and creating new infection centers (Filip 1990, Filip *et al.* 1992a).

What is the long-term prognosis for the area surveyed? In 1993, the western spruce budworm population declined dramatically. However, forest health will continue to decline as the amount of true fir continues to increase. The Deschutes National Forest has taken appropriate steps to improve forest health by replanting with pine and increasing prescribed burning. Natural fir regeneration within cutting units will need to be thinned to favor the pine, and overstocked areas surrounding

harvested units also need thinning. In central and eastern Oregon, precommercial thinning has been shown to reduce damage to residual true fir caused by defoliating insects, root diseases, and stem decays (Filip *et al.* 1992b, Wickman *et al.* 1992).

Because of aesthetic reasons, public concern, and new ecological data, the frequency of traditional clearcutting will decrease on the Deschutes and other National Forests in the Pacific Northwest, and the frequency of uneven-age and other even-age management systems will increase. Traditional thinning, seedtree or shelterwood systems, and their modifications or "new forestry" techniques can improve forest health if pest populations are recognized and less susceptible tree species are increased (Filip and Schmitt 1990).

Uneven-age management of eastside mixed conifers, however, often perpetuates true fir species and may lead to a decline in forest health; long-term research is needed to verify this hypothesis. Some beneficial effects of prescribed burning on root disease have been reported in central Oregon (Reaves *et al.* 1984, 1990), but further research is needed. Landscape-level research projects concerning the effects of forest practices on forest health are being established in Oregon through cooperation between land managers and scientists representing several agencies.

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Dennis E. Ferguson, Intermountain Research Station, USDA Forest Service, Moscow, Idaho 83843
and

David L. Adams, College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow, Idaho 83843

Effects of Pocket Gophers, Bracken Fern, and Western Coneflower on Survival and Growth of Planted Conifers

Abstract

This study was part of investigations on the Grand Fir Mosaic Ecosystem in northern Idaho that were undertaken because of poor regeneration success in harvested forests. Lack of regeneration appears to be related to high populations of northern pocket gophers (*Thomomys talpoides*), bracken fern (*Pteridium aquilinum*), and western coneflower (*Rudbeckia occidentalis*). This study quantified the effects of four treatments on survival and growth of planted conifers: unweeded with gophers, weeded with gophers, unweeded without gophers, and weeded without gophers. Subalpine fir (*Abies lasiocarpa*), grand fir (*Abies grandis*), lodgepole pine (*Pinus contorta*), and Engelmann spruce (*Picea engelmannii*) were planted at four study sites. After 3 years, Engelmann spruce and lodgepole pine had the lowest mortality from gophers, whereas grand fir and subalpine fir had the highest mortality. Most mortality caused by gophers occurred during the first summer and the first two winters after planting. Lodgepole pine was the tallest of the four species after 3 years; however, lodgepole pine appears to be susceptible to snow damage. Engelmann spruce is the recommended species for planting because of its good growth rate (even when growing with bracken fern and coneflower), low mortality from gophers, and its ability to withstand snowloads and senescing bracken fern.

Introduction

Both animals and plants have effects on the direction and rate of secondary succession in forest ecosystems. This seems especially true in the Grand Fir Mosaic Ecosystem where northern pocket gophers (*Thomomys talpoides*), bracken fern (*Pteridium aquilinum*), and western coneflower (*Rudbeckia occidentalis*) rapidly increase in cutover forests.

The Grand Fir Mosaic (GFM) is found in upland forests that form drainages for tributaries of the Clearwater River in northern Idaho. It is named for the dominant conifer, grand fir (*Abies grandis*), and the variety of sizes and shapes of natural openings in the forest canopy. Sitka alder (*Alnus sinuata*), bracken fern, and fool's huckleberry (*Menziesia ferruginea*) are the dominant species found in these openings. Investigations on this ecosystem were begun because of poor plantation success and the slow rate of secondary succession to woody vegetation (Sommer 1991, Ferguson 1991a).

The GFM encompasses approximately 200,000 ha, occurring as scattered blocks of land at elevations between 1,300 and 1,800 m. Forests at these elevations in northern Idaho are usually subalpine fir (*Abies lasiocarpa*) habitat types, but the GFM is warmer than expected. The predominant habitat type is *Abies grandis*/*Asarum caudatum*

(grand fir/ginger), a cool-wet habitat type as defined by Cooper *et al.* (1991). Forests in the GFM are located in areas that receive high snowfall during the winter months, but the volcanic ash-influenced soils are well drained. GFM forests are typically moist hillsides rather than riparian situations such as forest meadows.

The number of conifer species that occur in the GFM is limited when compared to adjacent forest types. Grand fir is found most often, followed by Engelmann spruce (*Picea engelmannii*) and subalpine fir. Douglas-fir (*Pseudotsuga menziesii*), western white pine (*Pinus monticola*), and western larch (*Larix occidentalis*) are found infrequently, and elevations in the GFM are too high for ponderosa pine (*Pinus ponderosa*). Western redcedar (*Thuja plicata*) and mountain hemlock (*Tsuga mertensiana*) are only found in certain parts of the GFM. Interestingly, lodgepole pine (*Pinus contorta*) is found at higher and lower elevations, but not in the GFM.

Table 1 shows an inventory of commonly found plant species in cutover forests in the GFM. These data were collected in 1989 from sites used in this study. Percent cover is a visual estimation of plot coverage for each species. Bracken fern has the highest average coverage, followed by strawberry (*Fragaria vesca*) and mitrewort (*Mitella stauropetala*). Woody species are infrequent on these sites, even though the areas were disturbed more than 14 years ago.

TABLE 1. Major plant species and average percent coverage for Grand Fir Mosaic sites used in this study.

Species	Common name	Percent coverage
<i>Asarum caudatum</i>	wild ginger	6.9
<i>Carex</i> sp.	sedges	7.8
<i>Cirsium</i> sp.	thistle	10.3
<i>Fragaria vesca</i>	strawberry	21.9
Grass	grasses	6.4
<i>Mitella stauropetala</i>	mitrewort	11.1
<i>Penstemon attenuatus</i>	penstemon	8.2
<i>Phacelia heterophylla</i>	virgate phacelia	2.0
<i>Polygonum douglasii</i>	Douglas' knotweed	8.6
<i>Pteridium aquilinum</i>	bracken fern	38.5
<i>Rudbeckia occidentalis</i>	western coneflower	9.3
<i>Symphoricarpos albus</i>	snowberry	8.0
<i>Vaccinium globulare</i>	huckleberry	8.3

Gopher populations are very high in the GFM. Gophers inhabit natural openings in the forest canopy, and their populations expand rapidly after forest disturbance. Three factors may contribute to high gopher populations in cutover forests: deep soils that contain volcanic ash, adequate soil moisture during the summer months, and the establishment of forb communities.

Gopher predation on conifers is a major concern for reforestation efforts throughout the western United States and Canada (Marsh and Steele 1992, Crouch 1971). Gophers tunnel through the soil feeding on forbs, shrubs, and trees (Teipner *et al.* 1983). Smaller trees are usually clipped near groundline with the top of the seedling then pulled from below into tunnels (Marsh and Steele 1992). Gophers may eat all or most of the root system of larger seedlings and saplings. This type of feeding may not become evident until the foliage turns brown or the tree begins to tip over (Marsh and Steele 1992). Under the snow, gophers clip and girdle the stems of trees.

While many herbaceous species are present following timber harvests in the GFM, bracken fern and coneflower have, by far, the highest amounts of above- and below-ground biomass. Bracken fern and coneflower reach heights of 1.5 to 1.8 m. Znerold (1979) calculated bracken fern frond density of 286,300 fronds/ha at Eagle Point, a site

we used in this study. Bracken fern is more abundant than coneflower in northern parts of the GFM while coneflower is more abundant in southern parts. In discussions that follow, bracken fern and coneflower will be abbreviated "PTAQ/RUOC" because they grow intermixed on the same sites.

Allelopathic potential has been demonstrated for bracken fern and coneflower (Stewart 1975, Gliessman 1976, Ferguson 1991b). Muller (1969) uses the term interference to include the effects of allelopathy and competition. Thus, removal of PTAQ/RUOC can demonstrate whether interference is occurring, but cannot evaluate the relative contributions of allelopathy and competition to reduced survival and growth of other plants.

It is difficult to determine the separate effects of gophers and PTAQ/RUOC where they occur together. A study was needed to separate these effects so the factors limiting successful reforestation could be determined. This study quantifies the separate and combined effects of gophers and PTAQ/RUOC on survival and growth of four planted conifer species for the first 3 years after planting.

Methods

Four study sites were chosen to represent GFM conditions. A summary of site conditions is given in Table 2. Three of the sites (Bertha, Dogleg, and Lytle) are located in clearcuts where the habitat type is *Abies grandis*/*Asarum caudatum*. The fourth site (Eagle Point) is located in a 1.5 ha natural opening where PTAQ/RUOC have probably dominated for hundreds of years, as evidenced by the current lack of woody vegetation and lack of charcoal in the soil.

Gopher exclosures at Eagle Point and Dogleg were constructed in 1987; those at Lytle and Bertha were constructed in 1988. At each site, a 15-by 15-m exclosure was constructed. Narrow trenches were dug 1 m deep around the perimeter. Soil from the trench was placed to the outside of the exclosure to minimize disturbance within the exclosure. Vertical wooden posts were placed into the trench to support 1.25-by 1.25-cm wire mesh. The wire mesh was nailed to the wooden posts so that the fence extended 1 m below ground and 1.5 m above the soil surface.

Soil was replaced in the trench, a wooden top rail was added, and a gate was built. Gophers were eliminated from exclosures by poisoning and

TABLE 2. Description of the four study sites.

Study site	Location	Elevation (m)	Aspect	Slope (%)	Study site history
Eagle Point	Clearwater N. F. North Fork District T40N, R7E, S35	1,400	East	20	Natural opening dominated by PTAQ/RUOC
Bertha	Clearwater N. F. North Fork District T39N, R5E, S1	1,200	South	20	Clearcut in 1975. No site preparation.
Dogleg	Nez Perce N. F. Selway District T31N, R6E, S23	1,740	South	5	Clearcut in 1973, bulldozer piled and burned in 1973.
Lytle	Nez Perce N. F. Elk City District T31N, R6E, S34	1,585	East	15	Clearcut in 1973, bulldozer piled and burned in 1976.

trapping. Poisoning or trapping gophers was done, if needed, each time exclosures were visited.

The fencing below ground kept gophers from digging through the soil into the exclosure. Fencing above ground kept gophers from tunneling through the snow into the exclosure or from traveling over the snow to enter the exclosure. The fence above ground was important because it was not possible to routinely inspect the exclosures for gopher activity during the winter.

Two additional 15- by 15-m plots were established at each site. These plots were treated the same as the exclosures except gophers were not excluded. Two non-exclosure plots were necessary because of anticipated higher tree mortality rates caused by gophers. These plots had enough surviving trees to compare growth rates with trees in the exclosures.

Each 15- by 15-m plot where gophers were not excluded was surrounded by a 1.25 m tall commercial snow fence made from vertical wooden slats. The snow fence helped prevent cattle and big game access. Also, the snow fence duplicated any effects the exclosure fence had on wind patterns or snow deposition.

Each plot was divided in half in the direction of the slope. One half was chosen at random to be weeded, beginning in the fall of 1988. Weeding was the physical removal of bracken fern and coneflower 2-3 times each growing season. Bracken fern fronds were pulled from the soil because digging up the rhizomes would have caused too much soil disturbance. Herbicides were not

used to kill bracken fern because rhizomes extending into the unweeded area might have been killed.

Coneflower plants were removed by severing lateral roots with a shovel, then lifting the caudex from the ground. Loose soil was shaken from the caudex into the hole where it had been removed.

All weeded material was deposited at least 1.5 m outside the fence, but never on the uphill side of the plot. This prevented leachates of decomposing plant material from affecting the weeded area. Weeding also included removing PTAQ/RUOC for 1.5 m outside the fence around the weeded half of the plot. The last weeding of each growing season was done in the fall before the rainy season.

Thus, conditions were created for four treatments: unweeded with gophers, weeded with gophers, unweeded without gophers, and weeded without gophers.

Containerized seedlings were grown in a greenhouse in Moscow, Idaho. Within species, the same seed source was used. Species were subalpine fir, grand fir, lodgepole pine, and Engelmann spruce. Subalpine fir, grand fir, and Engelmann spruce were chosen as test species because they are commonly found in the GFM. Lodgepole pine was chosen because it is a fast growing seral conifer that is found at higher and lower elevations in forests adjacent to the GFM.

Prior to planting, the greenhouse potting mix was gently shaken from the roots of the containerized seedlings. This insured that roots came into contact with the native soil when planted. Thus, the potting mix did not buffer the trees from chemical or physical properties of the soil.

Sites were planted in the spring of 1989. Four randomly chosen quadrats of 24 trees of each species were planted on each side of the enclosure (weeded and unweeded) and each non-enclosure. Spacing was 0.75- by 0.90-m. A row of border trees (a mixture of the same four species) was planted along the outside of the quadrats and between the weeded and unweeded portions of the plots.

Mortality and tree condition were recorded each spring and fall for the 2,304 trees. Tree heights were recorded each fall. Seedlings that had become entangled in senescing bracken fern fronds were uncovered in the spring and fall. Freeing these seedlings may have resulted in less mortality from the smothering effects of bracken fern, but it was necessary to determine seedling mortality, tree condition, and height. Whenever a tree was uncovered, this condition was recorded for later analysis.

A simple gopher activity index was recorded each spring. Six 4.6-m long line intercept transects were systematically laid out between the four test species; three each in weeded and unweeded areas. The index was the number of times the line intersected a winter gopher mound, soil plug, or cast.

Analysis

Gopher activity indices were analyzed using the General Linear Model (GLM) procedure in SAS (SAS 1985). The GLM procedure was used to perform analysis of variance and repeated measures analysis on these data. Differences between means were determined using Dunn's procedure at the 0.05 significance level. Indices entered into the analysis were spring counts for 1989-1992. The spring 1989 index characterized gopher activity at the time trees were planted.

Seedling mortality was also analyzed with GLM and Dunn's procedure at the 0.05 significance level. For each species, the ratio of dead trees was calculated for each quadrat of 24 trees 3 years after planting. The inverse sine transformation was used to analyze these binomial mortality data as suggested by Steel and Torrie (1960). The transformation also resulted in additivity of effects (no interaction between study sites and treatments) (Kirk 1982).

Seedling heights after 3 growing seasons were analyzed using GLM and Least Square Means (LSMEANS) (SAS 1985) for comparison of treatment means at the 0.05 significance level. Surviving trees were analyzed by species. Study site and seedling height at planting were included as independent variables in GLM and LSMEANS in order to account for their sources of variation. The result was a smaller error variance and a more powerful test to detect differences between treatment means (Kirk 1982).

Results

Gopher Activity Index

Fencing used to exclude gophers was most effective at Bertha and Lytle (Table 3). At the other two locations, fencing greatly reduced gopher activity. The averages shown in Table 3 reflect winter activity. During the summer, gopher activity was effectively controlled inside enclosures through periodic poisoning and trapping.

Winter gopher activity indices were examined as a repeated measures analysis because the same line transects were measured over several years. There was not a significant time effect at any of the study sites. Time-treatment effects were also non-significant except at the Dogleg study site. At Dogleg, gophers gained access to the enclosure and were more active in two measurement periods than in the other two periods.

TABLE 3. Winter gopher activity indices. Means are for four spring counts taken in 1989-1992, with three replications. Within study site, different letters indicate significantly different means at the 0.05 level using Dunn's test.

Gopher control	Weeding	Study Site				All 4 Sites
		Eagle	Bertha	Dogleg	Lytle	
Non-enclosure	Not weeded	3.12 ^{ab}	1.58 ^a	5.62 ^a	4.50 ^a	3.71 ^a
Non-enclosure	Weeded	4.58 ^a	2.29 ^a	5.46 ^a	3.88 ^{ab}	4.05 ^a
Enclosure	Not weeded	1.08 ^c	0.00 ^b	2.42 ^b	0.67 ^c	1.04 ^b
Enclosure	Weeded	1.83 ^{bc}	0.00 ^b	3.17 ^b	0.83 ^{bc}	1.46 ^b

TABLE 4. Percent of trees that died within the first 3 years after planting. Within species and cause of death, different letters indicate significantly different means at the 0.05 level using Dunn's test. Numbers in the table are percentages; however, the inverse sine transformation of the ratio of dead trees was used to determine differences between means.

Gopher control	Weeding	Species				All 4 species
		Subalpine fir	Grand fir	Lodgepole pine	Engelmann spruce	
Mortality due to causes other than gophers						
Non-exclosure	Not weeded	19.3 ^a	42.7 ^a	11.5 ^a	7.3 ^a	20.2 ^a
Non-exclosure	Weeded	23.4 ^a	44.8 ^a	1.0 ^a	8.3 ^a	19.4 ^a
Exclosure	Not weeded	26.0 ^a	49.0 ^a	3.1 ^a	12.5 ^a	22.7 ^a
Exclosure	Weeded	50.0 ^a	65.6 ^a	0.0 ^a	8.3 ^a	31.0 ^a
Mortality due to gophers						
Non-exclosure	Not weeded	46.4 ^{ab}	40.1 ^a	47.9 ^a	35.4 ^a	42.4 ^a
Non-exclosure	Weeded	63.5 ^a	42.2 ^a	45.3 ^a	38.0 ^a	47.3 ^a
Exclosure	Not weeded	10.4 ^c	20.8 ^a	20.8 ^a	6.2 ^a	14.6 ^b
Exclosure	Weeded	12.5 ^{bc}	22.9 ^a	6.2 ^a	5.2 ^a	11.7 ^b

Non-gopher Causes of Mortality

Of the four species tested, grand fir had the highest mortality from causes other than gophers (Table 4). Within the first month of planting, 34.2% of the grand fir were killed by voles (*Microtus* sp.). Voles stripped the bark off trees beginning at groundline and extending upward 5 to 8 cm. Mortality from voles occurred at three of the four study sites, the exception being Eagle Point. After 3 years, 50.5% of the grand fir were dead from causes other than gophers.

Subalpine fir had the next highest mortality rate (29.7%) from causes other than gophers. For most of these trees, we were unable to determine the cause of mortality, although the average size of subalpine fir at the time of planting was the smallest of the four species tested.

During the winter of 1991-1992, a fungus killed many seedlings of all species at Lytle. Damage appeared similar to a snow mold except the main stem of the seedling became blackened and was girdled.

Lodgepole pine and Engelmann spruce suffered the least mortality from non-gopher causes. Lodgepole pine averaged 3.9% and Engelmann spruce averaged 9.1% mortality after 3 years.

Mortality may have been higher if we had not uncovered seedlings that were smothered by bracken fern. Lodgepole pine was the species most often smothered by bracken fern, averaging 8.0%

for the 3-year period. For grand fir and Engelmann spruce, 4.2% of each species had been smothered. Only 1.0% of subalpine fir trees had been smothered by bracken fern.

Gopher-caused Mortality

Mortality caused by gophers is also summarized in Table 4. Subalpine fir had the highest rates of mortality caused by gophers, averaging 55.0% in non-exclosures.

Lodgepole pine had the second highest rate of mortality caused by gophers. An average of 46.6% of the seedlings were killed by gophers during the first 3 years in the non-exclosures.

Grand fir had the next highest rate of mortality due to gophers in non-exclosures, averaging 41.2%. Mortality would undoubtedly have been higher if voles had not killed many seedlings before gophers had a chance.

Engelmann spruce had the lowest mortality caused by gophers, averaging 36.7% in non-exclosures. Overall, spruce had good survival because of low gopher-caused mortality and low mortality from other factors.

The species preferences by gophers are masked by trees that died from other causes. Figure 1 shows the results of an analysis of mortality in non-exclosures where trees killed by causes other than gophers were not included. In these percentages, the numerator for each quadrat of 24 original trees

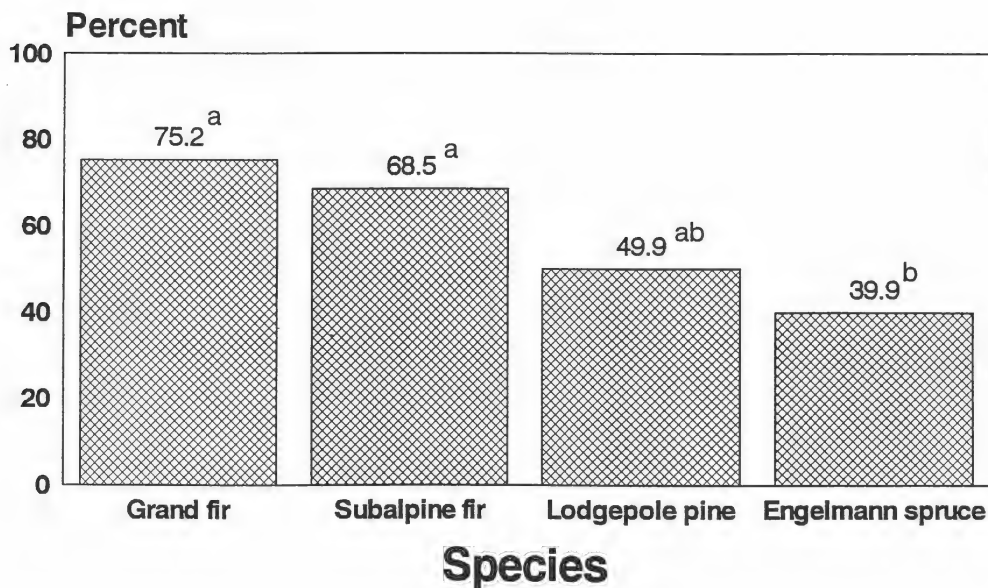


Figure 1. Average percent mortality due to gophers in non-exlosures. Percentages were calculated after eliminating trees killed by causes other than gophers. Means followed by different letters are significantly different at the 0.05 level using Dunn's test.

was the number killed by gophers and the denominator was 24 minus the number of trees killed by other causes. These results show the average percent killed by gophers in non-exlosures was 75.2% for grand fir, 68.5% for subalpine fir, 49.9% for lodgepole pine, and 39.9% for Engelmann spruce.

Gopher-caused Mortality by Time Periods

The percent of trees killed by gophers during summer and winter time periods is shown in Table 5. Data were obtained for each species by averaging mortality in the four study sites for each measurement period.

Mortality caused by gophers was highest the first summer and the next two winters after planting. Gopher-caused mortality was lowest in the second and third summer periods. For all four species, gopher-caused mortality averaged 13.0% the first summer, 15.0% the first winter, and 11.1% the second winter. Mortality the second and third summers averaged only 2.8 and 0.8%, respectively.

Fewer trees were killed by gophers during the third winter (1991-1992), but many trees were loose when gently tugged at groundline in the

spring of 1992. Prior to the spring 1992 measurement (3 years after planting), only one tree was recorded as being loose in the soil. The spring 1992 tally found 73 loose trees. Most of the loose trees were of the larger species—lodgepole pine and Engelmann spruce. Observations on a few of these trees showed that gophers had severed many, but not all, lateral roots.

Seedling Heights

Seedling heights at the end of the third growing season were analyzed by species. Only trees with no top damage were used in this analysis because trees with top damage mask height growth rates. Ninety-three trees were eliminated because of top damage: 29 subalpine fir, 19 grand fir, 30 lodgepole pine, and 15 Engelmann spruce. Tops had been chewed by animals or terminals had died from other causes.

Seedling heights after 3 growing seasons are shown in Table 6. These means account for study site and seedling height at the time of planting using LSMEANS (SAS 1985). The first trend evident was taller trees in the enclosures than in the non-enclosures, except for spruce. This provides

TABLE 5. Percent mortality due to gophers by time periods for non-exlosures.

Weeding	Time period					
	Summer 1989	Winter 1989/90	Summer 1990	Winter 1990/91	Summer 1991	Winter 1991/92
			Subalpine fir			
Not weeded	12.5	12.5	2.1	13.5	1.6	4.2
Weeded	12.5	35.4	4.7	8.9	1.0	1.0
			Grand fir			
Not weeded	17.2	5.7	4.2	9.4	0.5	3.1
Weeded	16.7	15.6	3.1	6.3	0.0	0.5
			Lodgepole pine			
Not weeded	11.5	16.1	2.6	14.6	1.6	1.5
Weeded	13.5	16.2	1.0	11.5	1.0	2.1
			Engelmann spruce			
Not weeded	7.8	9.4	2.6	12.5	0.0	3.1
Weeded	13.0	8.9	2.1	12.5	0.5	1.0
			All 4 species			
Not weeded	12.2	11.0	2.8	12.5	1.0	2.9
Weeded	13.9	19.0	2.8	9.7	0.7	1.2
Average	13.0	15.0	2.8	11.1	0.8	2.0

TABLE 6. Mean seedling heights (cm) at 3 years using LSMEANS (SAS 1985), which accounted for variation attributable to study site and seedling height at planting. Within species, means followed by different letters are significantly different at the 0.05 level.

Gopher control	Weeding	Species			
		Subalpine fir	Grand fir	Lodgepole pine	Engelmann spruce
Non-exclosure	Not weeded	14.7 ^b	34.6 ^{ab}	40.1 ^c	39.7 ^a
Non-exclosure	Weeded	16.0 ^{ab}	31.8 ^b	52.4 ^b	40.7 ^a
Exclosure	Not weeded	15.8 ^{ab}	39.4 ^a	49.5 ^b	42.0 ^a
Exclosure	Weeded	17.3 ^a	35.7 ^{ab}	59.9 ^a	39.7 ^a
Number of trees in analysis:		190	107	326	396

evidence that gophers negatively affect growth on seedlings they do not kill. Reduced growth is probably caused by partially devoured roots and/or soil disturbance.

For subalpine fir, weeding and gopher control had significantly positive effects on 3-year seedling heights compared to the control (gophers without weeding). However, subalpine fir is the slowest growing of the four species; weeding and gopher control only improved 3-year heights by 2.6 cm.

Grand fir was shorter in the weeded areas than in unweeded areas, although the differences were

not significant. The number of grand fir available for analysis (107) was lower than for other species in the study because of high mortality rates; further, the lowest number of grand fir seedlings was in the weeded areas. Grand fir were significantly taller in unweeded sections of exclosures (39.4 cm) than in weeded sections of non-exclosures (31.8 cm).

Lodgepole pine was the tallest of the four species after 3 years. Weeding PTAQ/RUOC resulted in increased heights of 10.4 cm in the exclosure and 12.3 cm in the non-exclosure, an average of

11.4 cm for weeding. Providing protection from gophers increased heights of surviving lodgepole pine 9.4 cm in the unweeded and 7.5 cm in the weeded areas, an average of 8.4 cm for gopher protection. With both weeding of PTAQ/RUOC and protection of trees from gophers, the gain in height averaged 19.8 cm after 3 years.

Engelmann spruce showed no statistically significant differences in heights among the four treatments. This is somewhat surprising and is an important finding. Evidently, neither gopher activity nor interference from PTAQ/RUOC was detrimental to height growth of Engelmann spruce.

Discussion

Mortality caused by gophers was highest during winter months, compared to summer months, except for the first summer after the seedlings were planted. High winter mortality to seedlings is consistent with other studies in the western United States (Marsh and Steele 1992, Crouch 1971). Therefore, the most important time to reduce gopher populations is just before winter. Eliminating or drastically reducing gopher populations in the fall should result in fewer seedlings killed during the winter.

High gopher-caused mortality following spring planting is circumstantial evidence that gophers found nursery-grown seedlings quite palatable. Another possibility is that nursery-grown seedlings have not developed enough defense chemicals to discourage gopher feeding.

Gophers preferred subalpine fir and grand fir over lodgepole pine and Engelmann spruce. Crouch (1971) found no gopher preferences among three pine species: ponderosa, Jeffrey (*Pinus jeffreyi*) and lodgepole pine, where two-thirds were killed by gophers within 3-1/2 years in south-central Oregon. Okello (1993) reported the highest gopher feeding preference for ponderosa pine, moderate preference for Douglas-fir, and lowest preference for western redcedar.

Where protected from gophers, planted seedlings in this study readily survived in plant communities dominated by PTAQ/RUOC. This is consistent with Dimock (1964), who reported 79% survival after 5 years for Douglas-fir seedlings planted in dense bracken fern; however, growth was reduced. Seedlings averaged only 45.5 cm tall after 5 years on a high site in western Washington.

Staeble *et al.* (1954) also reported that bracken fern reduced growth of Douglas-fir regeneration. Port-Orford-cedar (*Chamaecyparis lawsoniana*) regeneration had a moderate reduction in heights when growing in dense bracken fern, but western hemlock heights were not affected.

Conclusions and Recommendations

This study separated the effects of gophers from interference caused by PTAQ/RUOC. Even though it was not possible to keep all gophers out of the exclosures, their activity inside the exclosures was drastically reduced, resulting in reliable data.

None of the trees in this study appeared to die from allelopathy, probably because planting stock was large enough to buffer adverse soil chemical properties. Conversely, for natural regeneration, Ferguson and Boyd (1988) found that four species of conifer seed sown at the Eagle Point study site died after germination but before shedding seed coats. Natural regeneration is not a reliable reforestation option in the GFM.

We recommend planting 2 or 3 year old nursery stock with large basal diameter. Larger seedlings will survive better and become big enough to withstand gopher activity more quickly. Large caliper seedlings will withstand the smothering effects of bracken fern. Plant promptly after harvest before PTAQ/RUOC become tall and dense.

Interference from PTAQ/RUOC can slow growth of seedlings. Eventually, seedlings will overtop PTAQ/RUOC and shade them out. Of the four species tested, lodgepole pine was the most sensitive to interference from PTAQ/RUOC. Lodgepole pine growing in weeded areas of plots were significantly taller than those growing in unweeded areas.

Although lodgepole pine grew the fastest of the four species tested and is surviving well in the non-exclosures, we cannot recommend its widespread use for reforesting cutover forests in the GFM. Boyd and Znerold (in preparation) have found extensive snow damage to lodgepole pine planted at the Eagle Point study site in 1978. Snow has caused extensive damage to our gophers exclosures and to the snow fence that surrounds the non-exclosures. Perhaps lodgepole pine is not adapted to the kinds of snowpacks that occur in the GFM.

Grand fir was shorter in weeded areas of plots after 3 years, so there appears to be no advantage to weeding PTAQ/RUOC for grand fir growth.

Weeding PTAQ/RUOC also did not improve 3-year heights of subalpine fir.

Engelmann spruce 3-year heights were not significantly different in weeded versus unweeded areas or in exclosures versus non-exclosures. In addition, it had the lowest mortality from gophers, other causes of mortality were low, and it had the fewest trees with top damage. Although Engelmann spruce generally grew more slowly than lodgepole pine, it was as tall as lodgepole in the control where gophers were not excluded and PTAQ/RUOC were not weeded. We also observed that spruce is more resistant to being bent over by snow and senescing bracken fern. Engelmann spruce is the best choice among the four species tested for reforesting cutover forests in the GFM.

Engelmann spruce is commonly found in the GFM, and long-term survival of Engelmann spruce should be very good. Establishment of spruce plantations would appear to be the easiest way to reforest these sites; however, species diversity could

become a problem. To avoid monocultures, we recommend also planting other species and leaving seed trees of species other than Engelmann spruce on the site, especially if they are seral species such as Douglas-fir, western larch, or western white pine. These species may be able to regenerate in enough numbers to provide species diversity.

Gophers were more of a problem for planted trees than was interference from PTAQ/RUOC. Mortality is decreasing as the seedlings become larger, but many of the trees were loose in the soil after 3 years. This is evidence that gophers are still actively feeding on the root systems.

The critical times to reduce gopher populations would be the summer trees are planted and each fall until trees are large enough to survive despite gopher activity (about 10 years old [Marsh and Steele 1992]). This study will continue until at least 10 years after planting to allow monitoring of longer term survival and growth.

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R. B. Walker, Botany Department AJ-30, University of Washington, Seattle, Washington 98195

S. P. Gessel, College of Forest Resources AR-10, University of Washington, Seattle, Washington 98195
and

R. E. Miller, Forest Sciences Laboratory, U.S. Forest Service, Olympia, Washington 98502

Greenhouse and Laboratory Evaluation of Two Soils Derived from Volcanic Ash

Abstract

This study assessed the mineral nutrient status of two volcanic ash derived soils from SW Oregon. There are extensive areas of such soils in the Pacific Northwest, developed from prehistoric volcanic deposits. The study was initiated because conifers in some of the field plots on such soils had failed to give an expected yield response to the application of nitrogen fertilizer. Soil pot tests were carried out using both Romaine lettuce (*Lactuca sativa*) and Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] seedlings, with a wide range of fertilizer treatments. Heavy phosphorus fertilization was necessary for satisfactory growth of lettuce, which also showed a 26% response to sulfur addition. With Douglas-fir, pot tests showed no response to nitrogen alone, but gave a statistically significant response to phosphorus fertilization together with nitrogen (seedlings were non-mycorrhizal), and some suppression of yield with sulfur additions, probably from osmotic effects. There was a favorable effect of sulfur fertilization on foliar color, and a chlorosis in younger foliage probably attributable to iron deficiency. Most of the tissue analyses showed low concentrations of magnesium ($<0.05\%$), and also of calcium ($\leq 0.08\%$), iron ($<70 \text{ mg kg}^{-1}$), boron (mostly $<20 \text{ mg kg}^{-1}$) and copper ($\leq 2.6 \text{ mg kg}^{-1}$) in the younger foliage. Thus there is an implication from the field trials and evidence from the greenhouse and laboratory study that elements besides nitrogen need to be added to provide proper nutrition on these volcanic ash soils. This information can aid in guiding further fertilizer trials in forests on volcanic ash derived soil in SW Oregon and elsewhere.

Introduction

Research on forest soils in northwestern United States has demonstrated the importance of added nitrogen for optimal tree growth. Other elements also may sometimes be deficient, because concentrations of calcium, magnesium, phosphorus, sulfur, boron and even iron, molybdenum and zinc are often low in some soils and in forest tree foliage (Walker and Gessel, 1991; Zasoski *et al.*, 1990). Moreover, local agricultural experience demonstrates that sulfur deficiency often can limit crop growth, especially in soils derived from volcanic ash, and low sulfur supply may limit growth of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] at some locations (Chappell and Miller, 1988; Blake *et al.*, 1990). Soils derived from volcanic ash are extensive in the Pacific Northwest, with many originating from the Mt. Mazama volcanic explosion in the Oregon Cascade Range about 7,500 years ago. Substantial areas of these soils are in national forests which have been important timber-producing areas in addition to other values. Several fertilizer field trials on volcanic ash soils in the Rogue River National Forest in Oregon have shown variable response to nitrogen application (Opalach and Peterson, 1986).

This study was initiated, 1) to ascertain why in some instances there has been little or no response

in forest growth from addition of nitrogen fertilizer alone to volcanic ash derived soils, and 2) to determine if plant growth on such soils is stimulated by addition of one or more other essential mineral elements. Previously the usefulness of greenhouse studies with both tree seedlings and other plants for assessing the fertility status and fertilizer requirements of forest soils has been demonstrated (Vandecaveye, 1948; Walker and Gessel, 1991).

Thus two soils of volcanic ash origin were collected from areas of poor forest growth in the Rogue River National Forest in which growth response to nitrogen fertilization had been variable. Then greenhouse and laboratory studies were conducted using these soils to ascertain which mineral elements were in low supply or deficient. Douglas-fir seedlings were used for the main experiment, but Romaine lettuce (*Lactuca sativa*) plants were grown in a short-term preliminary trial. The results were expected to give guidance for improved multi-element fertilizer trials on plots in forests growing on volcanic ash soils in SW Oregon or elsewhere.

Methods

Locations of the collections, identified as soils I and II, are indicated in Table 1. The soil I collection

TABLE 1. Information on the two soils (from the upper Rogue River area, Josephine County, Oregon).

Soil	Collection area	Origin of soil	pH ^a	Organic matter ^c	Available p ^d	Total p ^e	Exchange Cations ^f					
							Ca	Mg	K	Na	cation esch. capacity	cation saturation
				g kg ⁻¹	mg kg ⁻¹	mg kg ⁻¹	-----c mol kg ⁻¹ -----					%
I	Lat. 42° 49' Long. 122° 29' W	Volcanic ash (13.7% rejected) ^a	5.5	21.7	21	870	2.7	0.29	0.41	0.11	10.8	33
II	Lat. 43° 5' N Long. 122° 20' W	Volcanic ash (13.6% rejected) ^a	5.1	26.8	20	830	0.80	0.09	0.13	0.13	7.8	15

^aSoils were passed through 2 mm square hole sieve before analyses

^bSaturation-paste method with water, using a Beckman model 76 glass-electrode pH meter (Richards, L.A., 1950).

^cDichromate oxidation procedure (Jackson, 1958)

^dTruog-type extraction (0.3%(NH₄)₂SO₄ in 0.002 N H₂SO₄) (Peech et al., 1947)

^eAmmonium acetate extraction (pH 7). Determination of cations by atomic absorption spectrophotometry.

^fExtraction with boiling 6 N HCl (Piper, 1944)

area was near the Pacific Northwest Stand Management Cooperative fertilizer installation 106 (Table 6). Soils were collected in autumn 1980 and sieved in the field to remove small pumice and organic fragments. This sieving removed less than 15% of the total volume, because the soils were not stony. The air-dried soils were analyzed for pH, organic matter content, available and total phosphorus, and exchangeable cations using standard techniques specified in the footnotes of Table 1. The fertilizer treatments (listed in Table 2) followed methods modified from Jenny *et al.* (1950). After thoroughly mixing the soil with liquid nutrient additions, according to the fertilizer treatment, the mixture was poured into one L plastic pots (13.7 cm top diameter) with moistened filter paper in the bottoms to cover drain holes; each pot was then placed in a saucer to collect and recycle any drainage water.

Pot Test Using Douglas-fir

Prior to potting in March 1981, one-year-old Douglas-fir seedlings from the U.S.D.A. Forest Service nursery at Medford, Oregon, were stored in a waterproofed paper bag for about one month at 5°C. Plants selected for potting had 11 to 13 cm long shoots and vigorous root systems; roots were trimmed to 12 cm. Occasional branch roots were also trimmed. Stem diameters just above the root collar were 2.0 to 2.5 mm. Some seedlings were obviously more vigorous, and most of these were deliberately planted as "controls" to ensure a con-

servative test of fertilization. Planting consisted of excavating a hole in the soil to accommodate the roots, then replacing the soil and adding water to ensure good root-soil contact. Treatments were prepared in six replications and "controls" in twelve replications.

The pots were distributed systematically on benches to ensure equivalent exposure to the greenhouse environment (at University of Washington, Seattle). Seedlings were periodically watered with distilled water, but excess watering was avoided. Early seedling mortality was about 10%, and dead seedlings were replaced with seedlings from refrigerator storage.

A considerable number of seedlings in soil I died in the ensuing months, so the remaining live seedlings were harvested in mid-November 1981. Plants in soil II, however, were maintained through the winter using fluorescent lights to extend day length to 16 hours. Plants were harvested from soil II in late June-early July 1982.

Measurements and Statistical Methods

At both harvests, the following measurements were recorded: height, diameter above root crown, and weights of older and younger needles, stems and roots after drying at 70°C. Visual appearance was also recorded. The yield values were evaluated statistically by both a standard t test and by using a Kruskal-Wallis non-parametric analysis (Zar, 1984).

Plant Tissues Analyses

After grinding, samples of leaf tissues were digested in strong nitric-perchloric acid. Analyses for macro- and micronutrient cations were made on an emission spectrophotometer (Jarrell-Ash Model 96-955 ICAP), and phosphorus was determined by the Zinzadze colorimetric procedure (Peech *et al.*, 1947).

Pot Test Using Romaine Lettuce (*Lactuca sativa*)

Tests with a rapidly growing herbaceous species can give quick indications of elemental deficiencies in soils. Fertilizer response in greenhouse pot tests needs to be substantial, however, to predict even modest response in the field. A lettuce pot test was set up, using the criteria of Vandecaveye (1948) for fertility evaluation. Only soil I was available in sufficient amounts for this test. Fertilization and soil handling were similar to that used with Douglas-fir. Romaine lettuce was sown on sand flats; when about 5 to 6-cm tall, one seedling was transferred to each pot of soil and allowed to grow for about six weeks in the University of Washington Botany Greenhouse. After harvest, leaves and stems were oven dried at 70°C, then weighed. Each treatment had four replicates.

Results and Discussion

Chemical Properties of Soils

Both soils were moderately acid, as expected. Soil I, with higher base status, was somewhat

higher in pH than soil II (5.5 vs. 5.1) (Table 1). Exchange capacity and concentrations of Ca, Mg, and K were markedly higher in soil I than in soil II. Although both soils were rather low in cation saturation percentage, that of soil II was lower. Organic matter content was similar in the two soils (Table 1).

Available Phosphorus

Various techniques can be used to estimate available phosphorus, but none of them are free of criticism. The Truog 0.002 N H₂SO₄ method, however, proved reasonably satisfactory in a study of 30 forest soils in Wisconsin (Kadeba and Boyle, 1978). Our values for soils I and II fell close to the mean in their study (19.7 ppm). Also as expected, the "available phosphorus" was a small fraction of the "total phosphorus" (Table 1).

Pot Test with Lettuce

With tree seedlings, growing for at least several months is needed to attain results, so this trial using Romaine lettuce plants was run for a quick early assessment of fertility. This proved to be useful, because the rapid growth of this herbaceous species accentuates any indications of low supplying capacity of the soil for the mineral elements.

Because of previous experience in growing lettuce on acid forest soils, lime was included in each treatment and phosphorus was added at high dosages. Growth rates were normal and yields were good (Table 2). In addition to a very marked

TABLE 2. Mean dry weights of Romaine lettuce grown on Rogue River Soil I

Treatment ^a	Mean Oven-Dry Weights (g) ^c			±SD ^b	% of NPKL
	Leaves	Stem	Total		
CaCO ₃ 2285 (=Lime)	—	—	0.12	0.04	3
N ₁₇₂ Lime	—	—	0.05	0.01	1
N ₁₇₂ P ₃₅₇ Lime	2.85	0.38	3.23	0.78	91
N ₁₇₂ P ₃₅₇ K ₅₇ Lime	3.19	0.37	3.56	0.72	100
N ₁₇₂ P ₃₅₇ K ₅₇ S ₅₇ Lime	3.95	0.52	4.47	0.51	126 ^d
N ₁₇₂ P ₃₅₇ K ₅₇ S ₅₇ B _{1.1} Lime	3.03	0.39	3.42	0.74	96

^aSubscripts refer to mg kg⁻¹ of N, P, K, S and B in the chemical form: N as NH₄NO₃; P as Ca(H₂PO₄)₂ and NaH₂PO₄; K as KCl; S as Na₂SO₄; B as H₃BO₃.

To convert mg Kg⁻¹ approximately to lbs Acre⁻¹, multiply by 2; to convert mg kg⁻¹ to kg ha⁻¹, multiply by 2.24.

^bSD = standard deviation

^cPlants grown for 6 weeks

^dPossible deficiency of sulfur indicated by this response using criterion of Vandecaveye (1948).

response to phosphorus, some response to potassium and to sulfur was apparent. Although lettuce could be expected to respond to both lime and phosphorus in the field, coniferous trees are not as likely to respond to such additions. Conifers are aided in their absorption of phosphorus by mycorrhizae, and the available-phosphorus concentrations seem to be in the range expected in forest soils. For lettuce, a further probable benefit of both liming and phosphorus addition is reduction in availability of potentially toxic aluminum and manganese; conifers, however, have high tolerance to these two elements even when present in appreciable concentrations (Radwan *et al.*, 1979; Porada, 1987). Response of lettuce to sulfur addition indicates that this soil has a low supplying capacity for this element. Forest tree growth may also be limited by low supplies of sulfur (Chappell and Miller, 1988).

Growth of Douglas-fir Seedlings

Probably as a result of the osmotic effects of added fertilizers, considerable mortality occurred during the early months, especially on soil I. Consequently, seedlings in soil I were harvested in November after 7 months of growth, whereas those on soil II were held over for additional growth to reduce the influence of the initial nutritional status of the seedlings. The results of the 7-month growth on soil I showed limited effects of fertilization, but there were indications of response to phosphorus (data not presented).

Seedlings in soil II grew well during the spring and early summer of 1982, and were harvested in July after 16 months of growth. Yields at harvest are presented in Table 3. Interpretations require caution because of the probable salt effects mentioned previously. Nitrogen alone did not

TABLE 3. Average seedling weights of Douglas-fir on Soil II by fertilizer treatments (grown March 1981 to July 1982).

Treatment ^a	Dry weight (g)						Relative total yield (%)
	Needles	Stems	Total shoot	Roots	Total plant		
					Mean	SD ^b	
Control	3.81	2.27	6.08	7.02	13.1	2.4	100
N ₁₀₇	3.55	2.33	5.88	5.83	11.7	4.7	89
N ₁₀₇ P ₄₇	4.94	2.86	7.80	6.32	14.1	2.5	108
N ₁₀₇ P ₉₃	4.93	2.56	7.49	6.02	13.5	2.1	103
N ₁₀₇ K ₄₄	3.49	2.21	5.70	5.01	10.7	2.4	82
N ₁₀₇ S ₅₃	3.79	2.23	6.02	5.55	11.6	1.3	89
N ₁₀₇ S ₁₀₇	3.76	2.48	6.24	6.31	12.6	1.5	96
N ₁₀₇ P ₄₇ K ₄₄	5.17	2.83	8.00	6.63	14.6	3.4	111
N ₁₀₇ P ₉₃ K ₄₄	5.80	3.28	9.08	8.30	17.4	2.2	133
N ₁₀₇ P ₉₃ K ₄₄ S ₅₃	5.50	2.80	8.30	6.62	14.9	3.1	114
N ₂₁₄	2.04	1.53	3.57	3.27	6.84	1.5	52
N ₂₁₄ P ₄₇	5.76	3.42	9.18	5.98	15.2	2.3	116
N ₂₁₄ P ₉₃	5.43	2.89	8.32	8.42	16.7	1.7	127
N ₂₁₄ K ₄₄	3.02	2.12	5.14	5.65	10.8	2.3	82
N ₂₁₄ S ₅₃	3.72	2.63	6.35	5.53	11.9	5.5	91
N ₂₁₄ S ₁₀₇	2.40	1.3	3.77	2.39	6.16	1.8	47
N ₂₁₄ P ₄₇ K ₄₄	4.68	2.57	7.25	6.25	13.5	2.6	103
N ₂₁₄ P ₉₃ K ₄₄	5.51	2.78	8.29	7.64	15.9	2.5	121
N ₂₁₄ P ₉₃ K ₄₄ S ₅₃	5.96	3.49	9.45	6.40	15.9	3.0	121
N ₂₁₄ P ₉₃ K ₄₄ S ₅₃ Mg ₅₄	5.20	2.84	8.04	5.11	13.2	2.6	101
N ₂₁₄ P ₉₃ K ₄₄ S ₅₃ Mg ₅₄ B _{1.1}	6.51	4.86	11.4	6.68	18.0	3.3	137

^aSubscripts refer to mg kg⁻¹ of N, P, K, Mg, S, and B added in chemical forms: N as NH₄NO₃; P as Ca(H₂PO₄)₂; K as KCl; S as Na₂SO₄; Mg as MgCl₂; and B as H₃BO₃ (mg kg⁻¹ x 2 = lbs Acre⁻¹, mg kg⁻¹ x 2.24 = kg ha⁻¹)

^bStandard deviation

TABLE 4. Relative growth and appearance of Douglas-fir seedling on selected treatments of Soil II at harvest.

Treatment ^a	Relative Growth ^b	Appearance and Symptoms	Possible Interpretation
Control	100%	1981 needles: green to light green. 1982 needles: short and yellow	Growth in 1981 was good, but in 1982 N was "exhausted"; some indication of an immobile-type deficiency.
N ₁₀₇ N ₂₁₄	89% 52%	Plants yellow-green; 1982 growth very short; some bronz- ing; N ₁₀₇ looks somewhat better than N ₂₁₄	N fertilization is unfavorable; osmotic effect may have been depressive; N may be suppressing P uptake.
N ₂₁₄ P ₄₇ N ₂₁₄ P ₉₃	116% 127%	1981 foliage green; 1982 extension good, although needles light green; the plants are among the best in the ex- periment; somewhat better than N ₁₀₇ P ₄₇ and N ₁₀₇ P ₉₃ .	Addition of P was definitely favorable, although possibly confounded by use of Ca(H ₂ PO ₄) ₂ ; yellowness of 1982 foliage may show low N, or possibly an immobile-type deficiency, likely Fe.
N ₁₀₇ P ₉₃ K ₄₄ N ₂₁₄ P ₉₃ K ₄₄	133% 121%	1981 foliage green; 1982 extension good, but needles light green.	No apparent response to K.
N ₁₀₇ P ₉₃ K ₄₄ S ₅₃	114%	1981 foliage: green; 1982 foliage: good growth but yellowish.	Osmotic depression is probably present, but the combination of N ₂₁₄ and S ₅₃ gave the best color in the 1982 needles.

^aSubscripts refer to mg kg⁻¹ of N, P, K, or S added in the chemical form: N as NH₄NO₃; P as Ca(H₂PO₄)₂; K as KCl; S as Na₂SO₄ (mg kg⁻¹ x 2 = lbs Acre⁻¹; mg kg⁻¹ x 2.24 = kg ha⁻¹).

^bPercentage of the total dry weight (roots + shoot) at harvest: ($\frac{\text{wt. of treatment}}{\text{wt. of control}} \times 100$)

improve yield and may have depressed growth in the N₂₁₄ (alone) treatment. This depression could have resulted from reduced phosphorus-uptake rather than nitrogen-depression. Phosphorus additions improved growth, especially where combined with N₂₁₄. Potassium addition did not improve yield consistently. Sulfur often improved foliar color but generally depressed yield, probably because of the salt influence. Magnesium did not improve growth, even though soil magnesium is low. The only treatment that included boron gave the highest yield in the experiment, but the large standard deviation suggested cautious interpretation.

The t test did not reveal any significant differences in mean yields. However the Kruskal-Wallis statistical analysis confirmed the interpretations stated above concerning phosphorus. With nitrogen-phosphorus treatments, yield increased significantly (0.025 level) and linearly with increasing phosphorus. Addition of other elements did not have statistically significant effects on yield, although with less variability among replicates, the trend toward a boron response might have been supported.

Some indications from foliar symptoms were interesting. With nitrogen fertilization alone, bronzing of needles was consistent. This indicated a probable phosphorus-deficiency (Table 4). Although phosphorus fertilization had a favorable influence, mycorrhizal development was visually weak or absent when the roots were washed out, so tree response to phosphorus in the field might not occur. However, this is uncertain since in southeastern United States, phosphorus deficiency has been reported in field trials even in the presence of mycorrhizae, and phosphorus fertilization is operationally used there (Allen, 1987; Pritchett and Comerford, 1982).

Current needles of control seedlings and those receiving both nitrogen and phosphorus were yellow or yellow-green in contrast with greener, older needles. Although this could be caused by slow redistribution of nitrogen, it suggests an immobile element deficiency, perhaps accentuated by phosphorus fertilization. Deficiency of iron is suspected, especially in view of the work of Perry, *et al.* (1984) who found iron limitation in Douglas-fir in pot tests with Douglas-fir on one soil from a site in SW Oregon which had been logged and burned, but not

TABLE 5. Elemental contents of Douglas-fir needles from selected treatments on soils I and II.^a

		Concentrations in dry needles								
Fertilizer treatment ^b	Sample	%				mg/kg				
		Ca	Mg	K	P	Fe	Mn	Cu	Zn	B
Soil I										
Control	Upper Leader	0.071	0.045	0.74	0.068	58	282	2.5	15	28
	Lower Leader	0.34	0.076	0.35	0.049	237	614	3.6	27	21
N ₁₀₇ P ₄₇	Leader	0.45	0.15	0.45	0.047	146	233	8.4	25	50
N ₂₁₄	Leader	0.69	0.20	0.59	0.06	157	352	9.8	29	74
N ₂₁₄ K ₄₄	Leader	0.72	0.19	0.80	0.057	143	397	7.3	30	33
N ₂₁₄ Mg ₅₄	Leader	0.87	0.40	0.38	0.081	203	463	—	31	63
N ₁₀₇ P ₉₃ K ₄₄ S ₅₃	Upper Leader	0.081	0.038	0.58	0.051	66	146	2.3	27	14
	Lower Leader	0.33	0.044	0.41	0.054	180	398	4.2	13	19
N ₂₁₄ P ₉₃	Upper Leader	0.31	0.061	0.29	0.049	97	454	4.1	26	16
	Lower Leader	0.68	0.086	0.25	0.046	315	389	5.1	42	33
Soil II										
N ₂₁₄ P ₄₇ K ₄₄	Upper Leader	0.067	0.031	0.67	0.042	55	258	2.1	14	19
	Lower Leader	0.32	0.050	0.35	0.043	204	573	4.1	31	16
N ₂₁₄ P ₉₃ K ₄₄	Upper Leader	0.093	0.036	0.47	0.045	62	289	1.6	14	13
	Lower Leader	0.57	0.070	0.39	0.053	213	1000	4.8	40	18
N ₂₁₄ P ₉₃ K ₄₄ S ₅₃	Upper Leader	0.10	0.054	0.47	0.055	66	217	2.6	15	10
	Lower Leader	0.44	0.046	0.28	0.059	200	833	5.2	29	17
N ₂₁₄ P ₉₃ K ₄₄ S ₅₃ Mg ₅₄	Upper Leader	0.097	0.12	0.44	0.051	69	416	2.7	15	12
	Lower Leader	0.60	0.29	0.23	0.055	261	1050	9.0	43	23

^aThese are of treatments in which visual symptoms were pronounced. "Upper leader" refers to the needles from the upper half of the leader, and "lower leader" to the needles from the lower half of the leader.

^bSubscripts have the same meaning as in Table 3.

in soils from undisturbed sites. Also Zasoski *et al.* (1990) found low concentrations of iron in Douglas fir growing in the field in western Washington. Sulfur additions often resulted in needle necrosis, probably from osmotic effects of the sulfate salt, but the best color in current foliage was in treatments which included N₂₁₄S₅₃. A favorable influence of sulfur-fertilization on needle color, and the tendency for current foliage to be lighter green in color than the older foliage, especially when phosphorus had been added, was noted with both of these soils.

Elemental Concentrations in Douglas-fir Needles

Tissue analyses were performed on selected treatments which from presence or absence of deficiency symptoms, yields, and uniformity of foliage seemed to be of particular interest, especially relating to phosphorus and to micronutrients. The results are presented in Table 5.

Soil I—Plants on soil I were grown during only one season and a favorable nutrient status when planted probably had a carryover influence. Some nutrient concentrations in the seedling foliage are of interest, however. Nitrogen fertilization apparently increased calcium and magnesium concentrations. Phosphorus was the only element in a deficiency range (<0.1%), as estimated by Walker and Gessel (1991).

Soil II—These results are more interesting because the seedlings grew longer, minimizing the influence of initial nutrient content, and the tissues were separated into younger and older needles. A number of trends are evident:

1. Calcium concentration was very low in the current foliage when potassium fertilizer was used. This is not too surprising, in view of the low concentration of exchangeable-calcium in the soil. Application of phosphorus as calcium phosphate did not increase calcium concentration in the foliage, probably because the amount of calcium applied in this form was small.

2. Magnesium concentration was also low in all foliar samples, except those from seedlings fertilized with magnesium. Because the soil is very low in exchangeable magnesium, low concentrations in tissue samples are not surprising, especially when potassium was added. Potassium competes with magnesium in absorption, so higher potassium reduces magnesium-uptake in Douglas-fir (Walker and Gessel, 1991).
3. Potassium was at medium concentrations in the current foliage of the control seedlings, but was relatively low in the older foliage. This suggests incipient potassium deficiency. Even in the potassium-fertilized seedlings, potassium concentrations of the older foliage were consistently lower than those of the current foliage, indicating that demand may have exceeded supply.
4. Tissue-phosphorus concentrations were low, even with phosphorus fertilization. This may be due to the well-recognized ability of ash soils to fix both native and fertilizer phosphorus (Macfarlane and Walmsley, 1977). Such fixation is also indicated by the relatively high "Total P" and low "Available P" (Table 1).
5. Tissue iron concentrations were low in the current foliage, and not very high in the older foliage. This may explain the chlorosis observed in younger foliage of plants on both soils.
6. Copper was in the range of expected deficiency in some of the samples ($< 3 \text{ mg kg}^{-1}$). Also the consistently lower values in current than in older foliage are indicative of deficiency of an immobile element.
7. Zinc and boron concentrations were not low enough to indicate definite deficiency (Walker and Gessel, 1991), although in most instances the boron concentrations were in a low range and less in upper than in lower foliage, suggesting incipient deficiency of this immobile element.

Relationship of These Results to Field Trials

A regionally coordinated program of forest fertilization field trials has been in place in the Northwest since the 1960s (Chappell *et al.*, 1991). Several installations had been established on the Rogue River National Forest but results were not available for guidance at the initiation of our current study. However, for comparison we selected three of the trials on volcanic ash soils near the collection areas for soils of this investigation, and for which growth data are available over a number of years since fertilization. Nitrogen at two levels was the only element tested in these trials. Results are given in Table 6.

TABLE 6. Initial stand characteristics and 8-year response to nitrogen fertilization at three locations in western Oregon with soils of volcanic ash origin.

Installation No.	Location	B.H. Age	50-yr site index	Thinning	RD	RDR ^a	N dosage	Growth (unfertilized)	Adjusted response (fertilized)	
		yr	m				kg ha ⁻¹	m ³ ha ⁻¹ yr ⁻¹	m ³ ha ⁻¹ yr ⁻¹	%
365	Lat. 42°44' N	21	27.4	no	11.2	1.07	220	22.1	-4.8	-20
	Long. 122°29' W			yes	4.3	1.20	220	10.5	0.3	3
106	Lat. 42°52' N	30	27.1	no	7.9	1.62	220	13.7	-0.1	0
	Long. 122°28' W			no		1.16	440	13.7	-0.7	-4
51	Lat. 42°44' N	42	25.9	no	15.3	1.04	220	16.2	2.6	15
	Long. 122°27' W			no		1.00	440	16.2	9.2	57

^aRDR = relative density ratio = RD of fertilized plots/RD of control plots; observed response was adjusted by this ratio.

RD 70 (English) = 10.1 (metric).

With only two replications at each fertilizer installation, combined with the variation in stocking in these stands (as reflected in the relative densities), gross generalizations are not possible. In the Douglas-fir region, a response to nitrogen fertilization is normally observed (Stegemoeller and Chappell, 1990; Chappell *et al.*, 1991), but here a clear response to nitrogen was seen only at Installation 51 (Table 6). Thus the field trial conclusions reinforce the greenhouse results, with both indicating that elements besides nitrogen need to be added to provide proper nutrition on these volcanic ash soils. Field trials can be improved by using results from short-term greenhouse screening tests to plan these elemental additions. However, combining results from many field trials to provide a wider geographic scope of inference is possible, as pointed out by Miller *et al.* (1988). They described results from 111 installations in Douglas-fir stands in Southwestern Oregon and 3 in Northern California which showed 70 percent responding to nitrogen. In this case the 30 percent not responding to nitrogen would need more specific research, such as pot tests and foliar analyses, to indicate which other elements are needed in a fertilization plan.

Conclusions

The study gave interesting insights into the mineral supplying ability of these volcanic ash derived forest soils, as follows:

1. Pot tests, soil analyses, and foliar analyses showed that the soils derived from volcanic ash used in this study are able to supply only low amounts of a number of mineral nutrients: calcium, magnesium, potassium, sulfur, phosphorus, nitrogen, copper and possibly boron and iron. At a given site and time, tree growth will

probably not be limited by a deficiency of more than one or two of these elements. If a deficiency of one element is corrected by fertilization, yield may still be limited by the supply of a second element, and so on. Such multiple deficiencies in the field may not show up until a future time after one or more additional harvesting cycles.

2. Pot tests and related laboratory analyses should not be used exclusively to make recommendations for extensive, operational field fertilization. Rather, they can be a good basis for guiding trials in nurseries or in the forest. In order to understand the full range of forest tree nutritional problems on these Rogue River volcanic ash soils, a coordinated series of nursery and field trials testing individual and combined elemental additions should be carried out. Analyses of field-collected needle samples from these trials could be compared with the pot test tissue analyses (Table 5) and with expected values (Walker and Gessel, 1991).
3. In both pot tests and field fertilization studies, rates of application need to be low or split dosages used to minimize osmotic effects in these light-textured volcanic ash soils.

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Hypogeous Sporocarps in Forest Remnants and Clearcuts in Southwest Oregon

Abstract

During June-August, 1991, we sampled hypogeous sporocarps on four late seral forest remnants ranging in size from 1.3 to 3.6 ha, and on clearcuts surrounding two of the remnants. In particular, our sampling of these southwestern Oregon sites (dominated by *Psuedotsuga menziesii*/*Abies concolor*) targeted three questions: 1) Are hypogeous sporocarps more abundant in remnants of late seral forest than in the surrounding clearcuts?; 2) Are hypogeous sporocarps more abundant under coarse woody debris?; 3) Is the California red-backed vole (*Clethrionomys californicus*) positively associated with areas having hypogeous sporocarps? Two forest remnants had twenty to forty times more hypogeous sporocarps than the young clearcuts which surrounded them. Hypogeous sporocarps were four times more abundant in plots having logs. Voles were more likely to be caught at traps having hypogeous sporocarps nearby. Remnant stands of late seral forest appear to provide a refuge for hypogeous sporocarps used by the California red-backed vole and other small mammals, and coarse woody debris may contribute to an abundance of hypogeous fungal sporocarps.

Introduction

The hypogeous sporocarps of mycorrhizal fungi (generally called "truffles"—Luoma 1988) are integral members of fully functioning Pacific Northwest coniferous forests. Truffles constitute the dominant food source of many small mammals, including 74%-89% of the diet of the California red-backed vole (*Clethrionomys californicus*) (Maser *et al.* 1978a; Ure and Maser 1982). Populations of *C. californicus* might become isolated on forest remnants in part because surrounding cutover areas lack truffles in early seral stages (Maser *et al.* 1978b; Ure and Maser 1982; Hayes *et al.* 1986). Although *C. californicus* is rarely found in young clearcuts (Gashwiler 1970; Mills In Press), it is not known whether suppressed truffle production might correlate with this absence of voles in clearcuts. Studying the distribution and abundance of truffles in a fragmented forest system will help foster understanding of the effects of fragmentation on *C. californicus*, and on other small mammals.

Furthermore, truffles have an ecological significance beyond supporting small mammals that rely on fungi in their diet. Nearly all hypogeous species form ectomycorrhizae with the roots of

vascular plants, and are particularly abundant in association with conifers in the Pacific Northwest (Trappe and Molina 1986; Castellano *et al.* 1989; Molina *et al.* 1992). Mycorrhizae ("fungus roots") greatly increase the amount of water and nutrients available to a plant in exchange for the plant's photosynthate (Harley 1969; Trappe and Maser 1978; Allen 1991). This mutualistic symbiosis is thought to be necessary for the survival of conifers in the Pacific Northwest (Perry *et al.* 1987; Luoma *et al.* 1991; Molina *et al.* 1992). Because red-backed voles and other small mammal mycophagists serve as the primary dispersal vectors for hypogeous taxa, truffles and their dispersers are therefore notable members of the forest's functional diversity.

While knowledge of truffle taxonomy and phenology have greatly expanded in recent decades, the ecological issues of mycophagy pertinent to management of the Pacific Northwest's fragmented forests remain poorly understood. We investigate the abundance of truffles on four late-successional forest remnants and the clearcuts surrounding two of them during the summer to explore three questions: 1) are truffles more abundant in late seral forest remnants than in young clearcuts?; 2) are truffles more abundant in association with coarse woody debris?; 3) is the California red-backed vole, *Clethrionomys californicus*, associated with areas having truffles?

Study Area and Methods

The four sites studied (Figure 1) are in the Klamath Mountains physiographic province, in locations that

¹Current address: Olympic National Park, Natural Science Studies, 600 E. Park Ave., Port Angeles, Washington 98362

²To whom correspondence should be addressed: Department of Fisheries and Wildlife, University of Idaho, Moscow, Idaho 83844

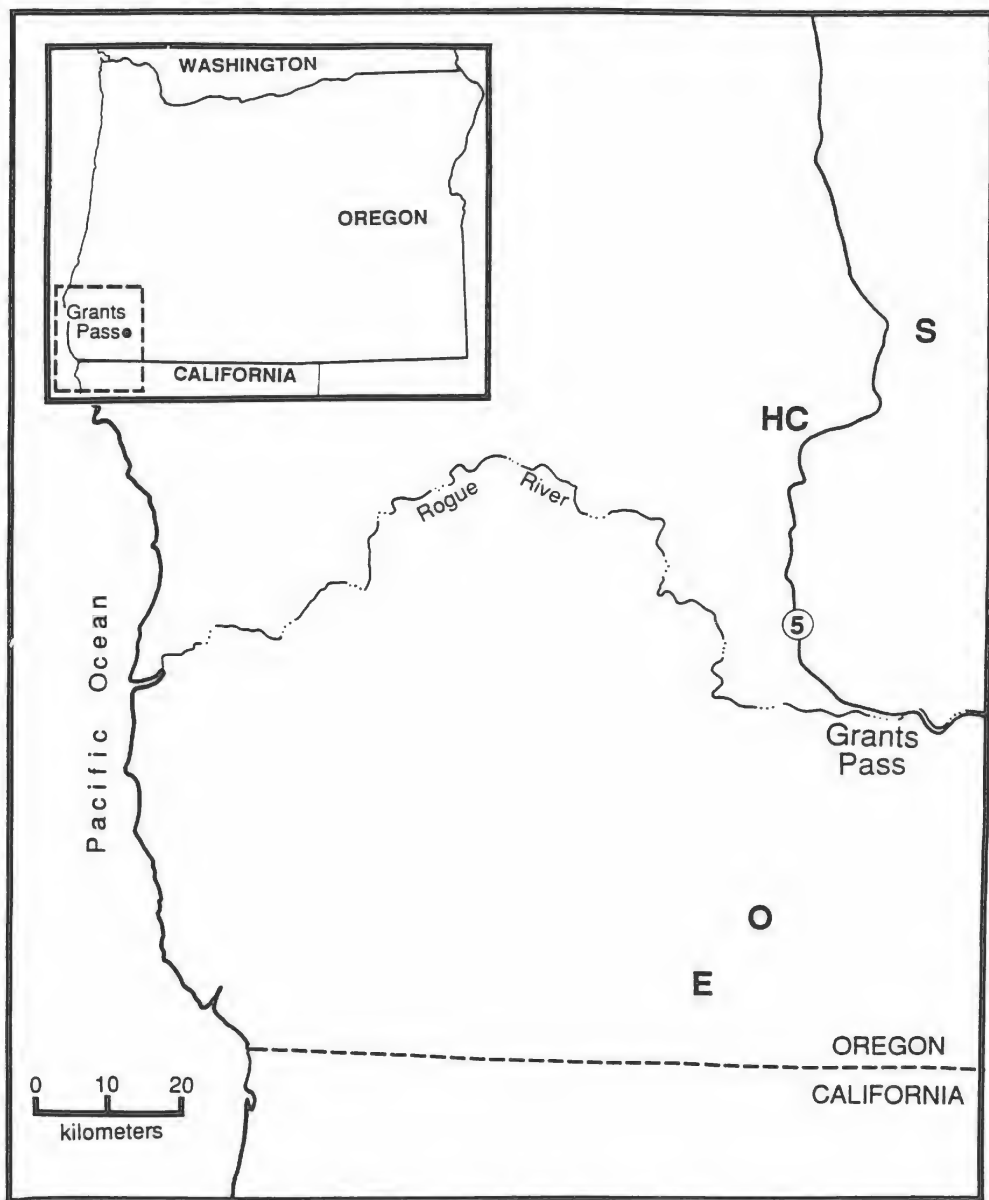


Figure 1. Location of four study sites sampled for truffles, 1991. The clearcuts surrounding sites E and O were sampled for forest-clearcut comparison. Map modified from Mills (In Press).

are relatively dry for the west side of the Cascades (mean annual rainfall 500-800 mm; Franklin and Dyrness 1973). Elevation, slope and aspect were variable, although all sites were steep and above

1,000 m (Table 1). All four sites were dominated by Douglas-fir (*Pseudotsuga menziesii*); the two higher sites (E and O) also had white fir (*Abies concolor*), and site HC had a tanoak (*Lithocarpus*

TABLE 1. Characteristics of sites sampled for truffles in southwestern Oregon, 1991. Modified from Mills (1993).

Site	Size (ha)	Number of truffle plots	Number of different trap sites with truffle plots ¹	Time since last cut	Distance (m) to nearest forest > 7 ha	Slope	Aspect	Elevation (m)
S	1.3	24	10	1977	150	33°	E	1032
HC	2.5	32	27	1974	95	24°	S	1007
E	2.5	40	40	1987	100	38°	W	1280
O	3.6	40	40	1981	150	31°	W	1402

¹On sites HC and S, a small mammal trap site might have more than one truffle plot; for the vole-truffle question, one of these truffle plots was randomly chosen for each trap site.

densiflorus) understory. All remnants, which ranged in size from 1.3 to 3.6 ha (Table 1), were completely surrounded by clearcuts <28 years old (see below).

We sampled truffle plots from mid-June until mid-August, 1991. For all three questions, each of the two treatments was sampled on alternate 1-4 day periods (if not on the same day) in order to eliminate the potentially confounding effects of weather. Each plot was 1x1 m in size, and was sampled by raking down to the organic-mineral soil interface. Truffles were weighed for fresh biomass within 24 hours and identified to genus.

Depending on remnant size, we sampled between 24 and 40 truffle plots on each remnant (Table 1). Placement of truffle plots was based on the systematic small mammal trapping grid of Mills (1993; In Press), which featured markers at measured 15-m intervals, indicating the locations of Sherman live traps. All truffle plots on remnants were placed within 5 m of randomly chosen trap markers, with exact placement constrained by avoiding rocky or densely vegetated areas.

To address our first question, whether truffle abundance in forest remnants differed from surrounding clearcuts, we also sampled the clearcuts around the two largest remnants (O and E, Table 1). The clearcuts were broadcast burned within two years of harvest and were 10 to 27 years old. These clearcuts are dominated by Douglas fir and white fir, although the percent cover by ectomycorrhizal host species is only about one-quarter that of the forest remnants (M. Amaranthus, U.S. Forest Service, Grants Pass, OR., unpubl. data). Because both remnants had 40 truffle plots each, we placed 40 plots throughout each surrounding clear-

cut. The clearcuts lacked a grid for systematic plot location, so each plot was located in the most promising microsites using the same criteria for placing plots within 5m of our randomly chosen locations on the forest remnants. Thus, we intentionally biased our test in favor of finding more truffles in clearcuts than in the remnants, which makes for a stronger test of the hypothesis that clearcuts have fewer truffles. Instead of performing pseudoreplicated statistical analysis of 80 plots in each of 2 remnants (Hurlbert 1984), we present our data for this question as graphical trends.

Second, we tested whether truffles are significantly associated with coarse woody debris within the forest remnants. If a downed log 10-70 cm in diameter was present within 5 m of a chosen marker flag, it was removed and the plot was placed underneath it. In this fashion, nearly half (43%) of all truffle plots were placed under logs. The proportion of log and no-log plots with at least one truffle present (occurrence) was compared using a 2X2 contingency test for binomial proportions (Rice 1988). To test whether fresh-weight biomass differed between log and no-log treatments we used a Behrens Fisher T-test (Rice and Gaines 1989). This test is preferred because it is robust to the unequal variances which commonly occur in ecological mycology research (Luoma 1988; 1991), including ours.

Finally, we asked if there was an association between truffle presence and the presence of California red-backed voles on the forest remnants. Based on small mammal trapping data collected the same summer as this study (Mills In Press), and on the conservative assumption that the home range of voles is 15 m in diameter (Tallmon and

Mills 1994), we tested whether plots with truffles tend to fall within vole home ranges more often than expected by chance. We first classified each truffle plot in all remnants as a "truffle present" or "truffle absent" plot. We then noted whether a California red-backed vole was captured in four nights of sampling in any of the five traps within 15 m of the plot. The null hypothesis, that plots with and without truffles have the same probability of having a vole present within 15 m, was tested with a 2x2 contingency test for comparing binomial proportions (Rice 1988).

Results and Discussion

We sampled a total of 136 truffle plots on four forest remnants, and 80 plots in clearcuts surrounding two of the forest remnants (E and O, Table 1). On the four remnants, 29 of 136 plots (21%) had at least one truffle, for a total of 82 sporocarps from 12 identified genera (Table 2). Weights varied greatly, with 3 of the 29 plots netting 51% of the total fresh-weight biomass on all remnants of 119.8g/136m².

TABLE 2. Total biomass and number of sporocarps for hypogeous sporocarp genera¹ found in 136 plots on four forest remnants sampled in June-August, 1991.

General	Total Biomass (g)	Number of Sporocarps
Melanogaster	40.5	6
Hysterangium	23.2	26
Gautieria	16.0	4
Genabea	10.0	20
Rhizopogon	3.7	4
Martellia	3.6	2
Gymnomyces	2.6	4
Genea	1.0	3
Octavianina	0.4	1
Tuber	0.2	1
Endogone	0.1	1
Leucophleps	0.1	1
Unidentified	18.3	9
TOTAL	119.8	82

¹Identified by Michael Amaranthus, U.S. Forest Service, Grants Pass, OR.

Truffle Production in Forest Remnants versus Adjacent Clearcuts

Late seral forest remnants "O" and "E" produced substantially more truffles than the clearcuts surrounding them (Figure 2). Nineteen of 80 plots on the two forest remnants had a total of 67 sporocarps, for a mean weight of 1.02 g (s.e. = 0.44) per plot. In contrast, the 80 clearcut plots had only a single truffle. To our knowledge, these are the first data to corroborate the "conventional wisdom" that hypogeous sporocarps are largely absent from young, slowly regenerating clearcuts.

Several interacting explanations probably account for our observation of truffles being virtually absent in clearcuts. First, decreased soil moisture on cutover areas may depress truffle production. Clearcutting and burning exacerbate soil dessication during the Northwest's summer drought (Chen *et al.* 1993), and truffle production tends to be lowest during hot and dry seasons (Fogel 1981). Similarly, the decrease in organic soil depth following clearcutting and burning can generate negative ecological effects (see Rosenberg *et al.* In Press), which could include a decrease in sporocarps normally found in the organic soil layer.

Low truffle abundance in clearcuts may also reflect reduced spore dispersal. In southwest Oregon, two primary dispersal vectors of hypogeous propagules, the California red-backed vole and Townsend's chipmunk (*Eutamias townsendii*), are significantly less likely to be captured in clearcuts than in forest remnants (Mills 1993, In Press). Finally, depressed truffle production may reflect the loss of plant hosts in these clearcuts. Most hypogeous fungi rely on ectomycorrhizal associations with conifers and ericaceous plants for nutrition (e.g., *Arctostaphylos* spp., *Arbutus menziesii*) (Trappe 1962; Trappe and Maser 1978; Perry *et al.* 1987; Molina *et al.* 1992), and a decrease of these hosts on clearcuts can greatly reduce ectomycorrhizae (Perry *et al.* 1987).

It is possible that other managed forests having substantive regeneration of ectomycorrhizal hosts may not show such dramatic losses of hypogeous fungal sporocarps. It is also possible that ectomycorrhizae may have formed on the few regenerating plants on our sites, but that the parent mycelia has not yet obtained sufficient photosynthate for fruiting. There is a great need for

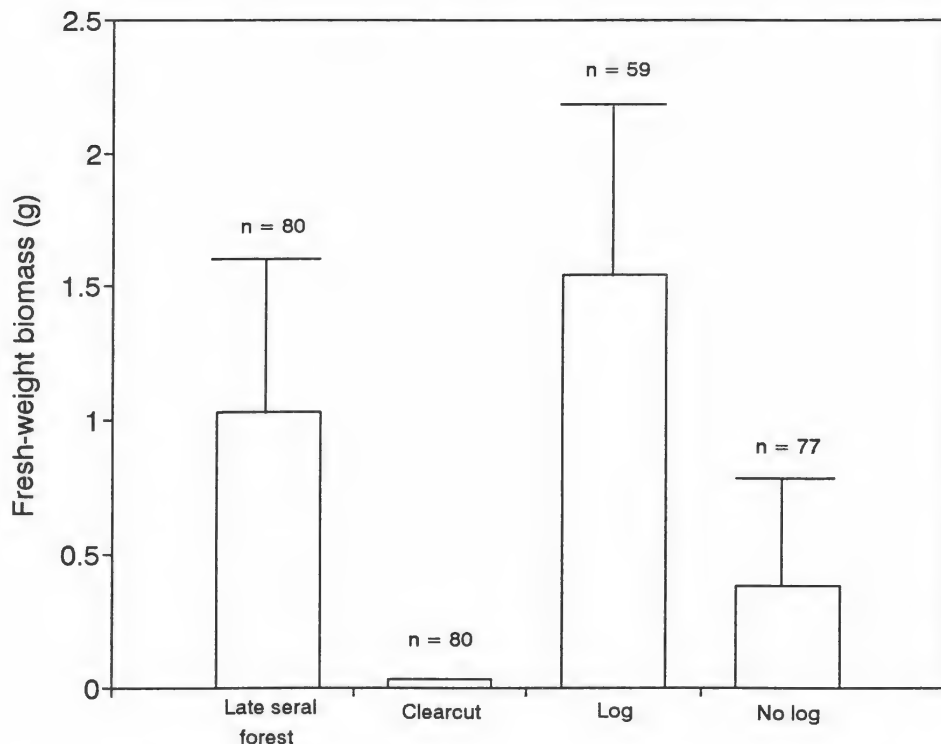


Figure 2. Mean (and standard error) of truffle fresh-weight biomass (grams). Comparisons include two late seral forest remnants versus their surrounding clearcuts, and log versus no-log plots on four forest remnants. Sample sizes refer to number of plots.

long-term study on mycorrhizal fungi in a variety of stand ages in order to determine the extent of fungal decline and regeneration in managed forests.

Truffles and Logs

Log plots were more than twice as likely to contain truffles than no-log plots ($P=0.007$). Similarly, truffle biomass was four times greater in log than in no-log plots (Figure 2), although high variance made statistical significance marginal ($P=0.08$).

Harvey *et al.* (1976) had a similar finding in western Montana, where mycorrhizae were found in greater amounts underneath logs. However, Luoma (1988) was the first to investigate any relationship between production of sporocarps and logs; his multi-year, year-round study in the relatively mesic westside Cascades found no significant correlation between logs and increased truffle production. This at first seems unexpected since

logs are primary habitat for mycophagous small mammals who presumably inoculate these areas with feces laden with spores of mycorrhizal fungi (Franklin *et al.* 1981; Luoma 1988).

Nevertheless, logs may be uniquely important for truffles and voles in southwestern Oregon since the soils are relatively dry and poor (Franklin and Dyrness 1973; Hayes *et al.* 1986). Because logs provide a reservoir of moisture for surrounding soils during months of little precipitation, they serve increasingly vital ecological functions in drier regions (Franklin *et al.* 1981; Maser and Trappe 1984). For example, radio-telemetry on California red-backed voles on one of our sites (Site E) during the same summer found that 98% of telemetry locations for four voles were under logs, even though logs covered only 7% of the vole home range area; also, more highly decayed logs were preferred (Tallmon and Mills 1994). Preferential log use by this mycophagist would inoculate

log-covered soils with spores of hypogeous taxa, explaining in part why more sporocarps are found there as well. We find it likely that this study found a positive log-truffle relationship where Luoma did not because the drier summer climate of southwestern Oregon tends to result in association of both moisture and mycophagy around coarse woody debris.

Truffle Occurrence Related to Vole Occurrence

Of the 136 total truffle plots, 19 were deleted from this analysis (with the deleted plot chosen randomly) because they represented multiple samples at the same trap location (Table 1). Of the 117 truffle plots at different trap locations, we found that red-backed voles were more likely to occur in areas with truffles than in those lacking them ($P < .05$; Table 3). For plots with truffles, 78% (28 of 36) had voles within a 15 m radius around the truffle plot. For plots lacking truffles, 46% (37 of 81) had voles within a 15 m radius.

TABLE 3. Contingency table showing plots with or without truffles having California red-backed voles within 15 m.

	vole	no vole	total
truffle	28	8	36
no truffle	37	44	81
total	65	52	117

The finding that voles tend to be found near truffles corroborates earlier research showing that the California red-backed vole's fecal pellets are composed mostly of spores from hypogeous sporocarps (Maser *et al.* 1978a; Ure and Maser 1982). The finding that voles are often found near truffles, coupled with our observations that both voles (Mills In Press) and truffles are nearly absent from clearcuts, strengthens earlier suggestions that "dependence on [hypogeous] ectomycorrhizal fungi by the western red-backed vole probably accounts for the latter's disappearance from deforested sites" (Ure and Maser 1982: 3307).

Although our results are limited to the summer period, this is the time for both maximum truffle consumption for the California red-backed vole in southwestern Oregon (Hayes *et al.* 1986), and the

most limited period of fruiting of hypogeous fungi in general (Fogel 1976; 1981). Thus, these small remnants of forest may be especially important to red-backed voles during the dry season.

Conclusion

We found that during the summer of 1991 truffles were practically absent from young clearcuts in comparison to adjacent forest remnants. On remnants, truffles were more often found under logs and near red-backed voles. Our findings may be most relevant to the drier forests of southwestern Oregon and northwestern California, and there is certainly need to examine these questions over a wide variety of sites, seasons, and years. Nevertheless, it appears that small remnants of late seral forest can serve, at least seasonally, as vital refuges for hypogeous sporocarps and the small mammal mycophagists (Mills 1993) which eat and disperse them. Logs seemed to be an important structure for maintaining an abundance of truffles and red-backed voles on our forest remnants (see also Tallmon and Mills 1994, Mills In Press). Our study strengthens other suggestions that coarse woody debris may be central to maintaining biological and functional diversity across fragmented landscapes, in both managed and unmanaged forests (Franklin *et al.* 1981; Spies *et al.* 1988; Spies and Cline 1988; Hansen *et al.* 1991, Tallmon and Mills 1994).

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Habitat Associations of California Red-backed Voles in Young and Old-Growth Forests in Western Oregon

Abstract

Because of the reduction of old-growth forests in the Pacific Northwest, and the controversy over timber management practices, patterns of animal abundance in young and old forests have gained attention. Results from previous studies on California red-backed voles (*Clethrionomys californicus*), however, have been inconsistent; unmanaged young stands were reported to have similar abundance of California red-backed voles as old-growth stands, while other studies suggested that numbers are higher in older stands. We compared California red-backed vole abundance in 5 young (30-60 yr old) and 5 old-growth (>400 yr old) Douglas-fir (*Pseudotsuga menziesii*) stands in the central Oregon Cascade Range during spring 1988-1991. The average number of California red-backed voles captured was consistently higher in old-growth stands ($\bar{X} \pm \text{SE}$, 8.4 ± 1.9) than in young stands (2.0 ± 0.8) during the 4 years of the study; 80% of the voles captured in the 5 young stands were from one unmanaged, fire regenerated stand. Our results support hypotheses of lower abundance of California red-backed voles in managed young forests than in unmanaged older forests. Providing components of old-growth forests, such as deep organic-soil depths, residual large trees and snags, and coarse woody-debris in managed young stands will likely increase their potential as suitable habitat for California red-backed voles.

Introduction

California red-backed voles (*Clethrionomys californicus*) are endemic to forests in western Oregon and northwest California (Alexander and Verts 1992). Some investigators suggested that California red-backed voles occur more frequently in mature closed-canopy forests with little understory development, and select for habitat that has significant amounts of coarse woody debris (Tevis 1956, Gashwiler 1959, Maser 1981, Doyle 1987, Gomez 1992), or greater food resources (hypogeous fungi, Ure and Maser 1982). Other investigators did not detect a difference in abundance of California red-backed voles between young and older forests (Aubrey *et al.* 1991, Corn and Bury 1991, Gilbert and Allwine 1991). However, young stands examined in the latter studies were naturally regenerated after fire, and the authors suggested that California red-backed voles may respond differently to managed second-growth stands that originated from clear-cuttings.

The controversy over extensive harvesting of Pacific Northwest forests (e.g., Thomas *et al.* 1988, Booth 1991) has led to extensive investigations of wildlife associated with older forests (e.g., Ruggiero *et al.* 1991). In this paper, we report our findings on the abundance and habitat associations of California red-backed voles in young and old-growth forests in the Cascade Range in central Oregon and discuss our findings in relation to previous studies of this species in unmanaged (natural) young stands.

Methods

We selected 5 young (30 to 60 years old) and 5 old-growth (>400 years) forest stands in the Blue River and McKenzie Ranger districts, Willamette National Forest, located in the central Oregon Cascades. Stands were dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Stands were between 375 and 900 m elevation; slopes ranged from 10 to 60%. Climate in this region is characterized by mild, wet winters and warm, dry summers (Franklin and Dyrness 1973).

Four of the 5 young stands resulted from planting after clear-cutting; the fifth stand was naturally regenerated after a wildfire in 1918 (Teensma 1987). Three of the 4 stands that were planted following harvest were broadcast burned. The records for the fourth stand were incomplete. Silvicultural treatments of the 4 planted stands varied from intensive clear-cuttings with no residual large trees to those with some large trees retained (1.2 trees >79 cm diameter at breast height (dbh)/ha). The 5 old-growth stands were not logged previously except for small areas where a few individual trees had been salvaged; <5% of the basal area was removed. Details of stand histories are given in Rosenberg and Anthony (1993).

We established 10 X 10 live-trapping grids (3.2 ha) in each of the 10 stands. Each grid consisted of 100 Sherman live-traps (7.6 X 7.6 X 25.4 cm) spaced at 20-m intervals. Traps were baited with oats and peanut butter and set for 8 consecutive

nights on 2 grids (1 old and 1 young) simultaneously for 5 trapping sessions each year during April to June, 1988-91. Captured California red-backed voles were toe-clipped for individual recognition and released.

We used nested circular-plots modified from Spies *et al.* (1988) to sample vegetation at 80–120-m intervals centered at trap stations; a total of 329 plots was sampled (approximately 33 per stand). Samples were collected during July–September 1988 from a 13-ha grid that included the trapping grids; this larger grid was used in studies of northern flying squirrels (Rosenberg and Anthony 1992). In order to reduce the number of vegetation variables originally measured (Rosenberg 1991), we selected those that we believed to be most important biologically to California red-backed voles. Numbers of large (≥ 50 cm diameter) trees, snags (≥ 1.5 m tall), and fallen trees (coarse woody debris) were recorded in 0.12-ha (20-m-radius) plots centered at 40-m intervals. Smaller trees (5–49 cm dbh) and coarse woody debris (25–49 cm diameter) were measured in 0.05-ha (12.6 m-radius) plots. We recorded the species and diameter at breast height (dbh) of live trees and snags; with coarse woody debris, we recorded the diameter (mean of the 2 ends), % bark remaining, and the percent of the surface that was charred. Volume of coarse woody debris (m^3) was computed for fallen trees ≥ 25 cm in diameter (Rosenberg 1991). We computed the proportion of the coarse woody-debris volume that was considered in a late decay state (no bark remaining) and the proportion of the number of observations of coarse woody-debris that was not charred.

Percent cover of understory plants, ground cover of herbs, fine woody debris (< 25 cm diameter), and moss was estimated visually in 8 1-m^2 quadrats within the circular plots. These were placed 4 and 7 m from the trap station along each cardinal direction. We calculated the mean of the values from the 8 quadrats and used these data in our analyses. In the same quadrats, organic soil depth ≤ 10 cm (including litter) was measured to the nearest 1 cm; greater depths were recorded as > 10 cm. The median value of soil depth from the 8 samples was used in the analyses.

Statistical Analyses

We compared the number of voles captured between stand age-classes with a split-plot analysis

of variance (Sokal and Rohlf 1981:394) with stand nested within stand age-class and year (where appropriate) as the error term. We used the number of individuals captured as a measure of relative abundance. This method was used rather than estimating actual abundance from mark-recapture data because numbers of captures and recaptures were low in young stands. The number of individual voles captured was log transformed.

Relationships of vole abundance to habitat characteristics were evaluated with regression and principal components analyses (PCA). Because of the correlated nature of the habitat variables, we derived a new set of uncorrelated variables from the habitat values from each stand using PCA. We examined the relationship of habitat (using the first principal component scores) and California red-backed vole abundance (total of the 4 years, log transformed) with linear regression analysis. We compared the proportion of the volume of coarse woody-debris without bark and the proportion of coarse woody-debris that was not charred between stand age-classes with Student's *t*-test after arc sine square-root transformation. The mean and standard error presented were those prior to transformations.

Results

We captured 209 individual California red-backed voles during the 4 years of the study. There were significantly more voles captured in old-growth ($n = 168$, 80.4%) than in young ($n = 41$, 19.6%) stands ($F_{1,8} = 7.8$, $P = 0.02$). There were no voles captured in 3 of 5 young stands in each year (Figure 1), and voles were never trapped in 1 young stand (Y-4, Figure 2). Most captures in young stands (33 of 41, 80%) occurred in 1 grid (Y-1, Figure 2). There was no consistent trend in abundance during the 4 years of the study; in a given year, the number of voles increased in some stands, but decreased in others (Figure 1). Therefore, year was not a statistically significant variable in explaining patterns of vole abundance ($F_{3,24} = 1.7$, $P = 0.18$).

Habitat characteristics differed between stand types; young and old-growth stands were separated primarily along the first principal component (Figure 3). The unmanaged young stand (Y-1), which had originated from wildfire, was more similar to the old-growth stands than the managed second-growth stands (Figure 3). The first principal

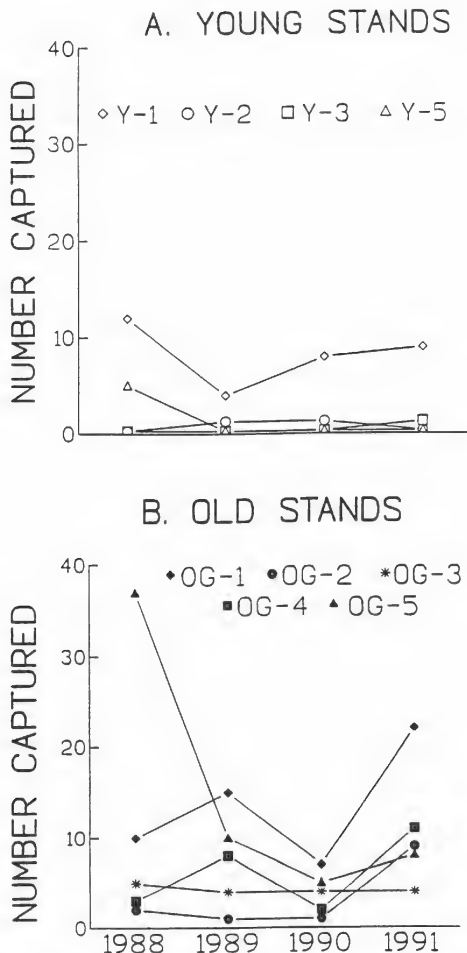


Figure 1. Fluctuation of number of individual western red-backed voles captured in (A) 4 young (Y) and in (B) 5 old-growth (OG) stands during spring 1988-1991, Willamette National Forest, Oregon. Not shown is the 1 young stand (Y-4) in which we did not capture any voles.

component explained 44% of the variation of the measured habitat variables among stands; the second added 21%, and each additional PC added $\leq 10\%$. The first principal component represents a gradient of increasing density of large trees and large snags, and increasing organic soil depth; the second PC was most related to increasing shrub cover (Table 1). California red-backed vole abundance (log transformed) was correlated positively

with the first principal component scores ($r = 0.84$, $P = 0.003$, $n = 10$; Figure 4).

Although there were large volumes of coarse woody-debris in young and old-growth stands (Rosenberg and Anthony 1992), a higher proportion seemed further decayed (lacked bark) in young (0.71 ± 0.04) than in old-growth stands (0.37 ± 0.03 ; $t = 6.1$, $df = 8$, $P = 0.0003$). However, a higher proportion of the observations of coarse woody debris in old-growth stands (0.95 ± 0.02) did not have evidence of char compared to coarse woody-debris in young stands (0.36 ± 0.07 ; $t = -7.7$, $df = 8$, $P = 0.0001$).

Discussion

Although recent studies indicated that California red-backed voles were as abundant in unmanaged young stands as in old-growth stands (Aubrey *et al.* 1991, Corn and Bury 1991, Gilbert and Allwine 1991), this result was not found in managed young stands in our study. We found significantly higher numbers of voles in old-growth compared to managed young stands, with a paucity of voles in the latter type. We did, however, find similar California red-backed vole abundances in the 1 fire-regenerated young stand (Y-1) as in the old-growth stands. Although there are currently many sites where California red-backed voles reach high abundance (e.g., in old growth and unmanaged [natural] young stands), they will likely become less abundant as the forested landscape continues to change from old growth to managed young forests through intensive timber harvesting activities.

Two of the 3 habitat variables (density of large trees and snags) that characterized the first PC were those usually associated with old-growth Douglas-fir forests (e.g., Franklin and Spies 1991). These two variables also characterized older stands in Corn and Bury's (1991) study; however, they found no difference in vole abundance between young and older forests. Thus, California red-backed vole abundance may not be related directly to density of large trees and large snags. Forest floor conditions seem to be more predictive of high California red-backed vole abundance, which is not surprising considering their natural history: they nest in underground burrows or under debris (Stephens 1906:124), often forage in the organic layer of soil (Maser 1981), and use coarse woody-debris for cover, as travel corridors, and as a source of sporocarps of mycorrhizal fungi (Hayes and Cross 1987, Tallmon and Mills 1994).

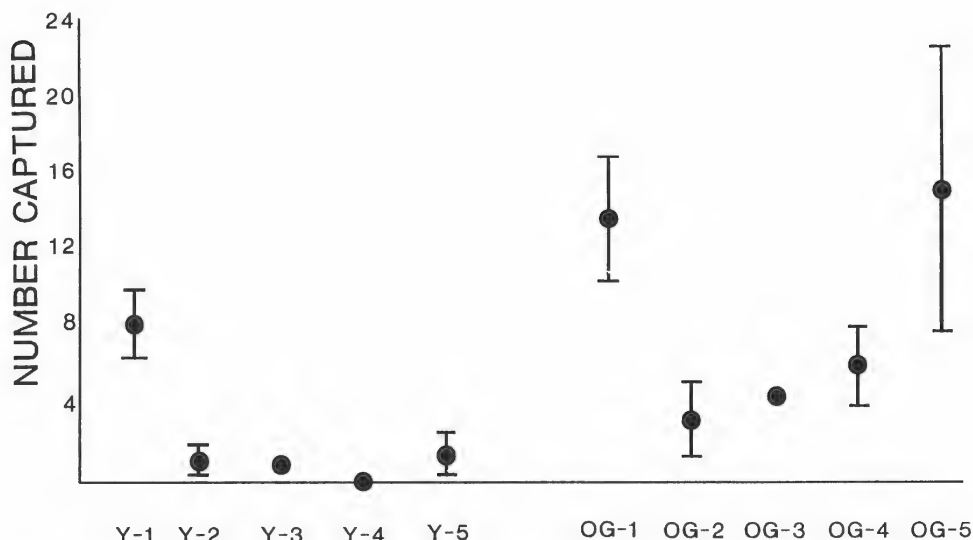


Figure 2. Number of individual western red-backed voles ($\bar{X} \pm \text{SE}$) captured in young (Y) and old-growth (OG) stands during spring 1988-1991. The SE represents the yearly variation in number of individual voles captured.

The presence of a deep organic soil layer may add significantly to forest-floor conditions for California red-backed voles. Our findings suggest that this is an important component in providing suitable habitat. Similarly, organic soil depth was correlated positively with California red-backed vole abundance in the Oregon Coast Ranges (Gomez 1992). Past fire histories of stands may be related to current organic soil depths. Prescribed broadcast-burning can reduce organic soil depth by consuming organic matter, volatilizing nutrients, and increasing erosion (McNabb and Cromack 1990, McNabb and Swanson 1990). In our study, depth of the organic soil layer in the young stands that were broadcast burned averaged 2.4 cm, while depth in the old-growth stands averaged 7.9 cm (calculated from values in Rosenberg and Anthony 1992). California red-backed voles were captured infrequently in these young stands. The 1 young stand (Y-1) in which we consistently found voles had originated from a low intensity wildfire (Teensma 1987); the average organic soil depth in this stand was 7.8 cm. The old-growth stand (OG-2) that had low numbers of voles also had low organic soil depth (4.9 cm), probably due to erosion from the steep slope (60%) of the stand. Shallow organic soil depth may help explain why California red-backed voles are not common in re-

cent clear-cuttings following prescribed burning (Tevis 1956, Gashwiler 1959, 1970; Hooven and Black 1976).

Although coarse woody-debris has been suggested to contribute significantly to California red-backed vole abundance (Tevis 1956, Maser 1981, Doyle 1987, Gomez 1992), our findings suggest that other attributes of the forest-floor may be more significant biologically. All of the young stands in our study had large volumes of woody debris (Rosenberg and Anthony 1992), yet red-backed voles were generally absent. Research on specific use of coarse woody debris by California red-backed voles demonstrated that large logs are used selectively over smaller logs (Hayes and Cross 1987), and that an increased decay state of coarse woody-debris was selected over less decayed woody debris (Tallmon and Mills 1994). These conditions seem to have been met in the young stands we examined, although the influence of char on quality of coarse woody-debris for California red-backed voles is unknown. Forest-floor conditions, including coarse woody debris (Tallmon and Mills 1994) as well as depth of organic soil, are likely to be critical components of the forest for providing high quality habitat for California red-backed voles.

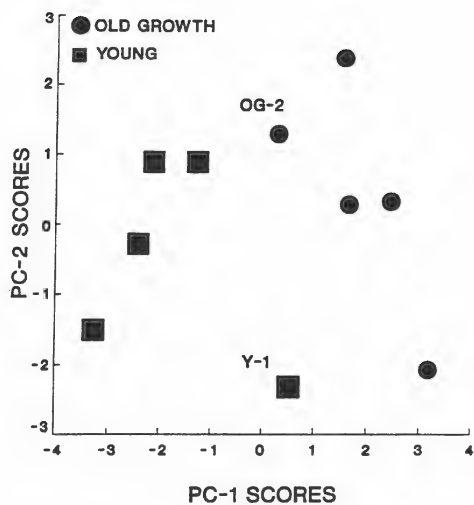


Figure 3. Young and old-growth stands plotted along the first 2 principal components. The first PC represents a gradient of increasing density of large trees and large snags, and increasing depth of the organic soil layer. The second PC was related most heavily to increasing shrub cover. Y-1 and OG-2 are the young and old-growth stands, respectively, that had mean number of voles captured most different from the other stands within their respective stand age-class.

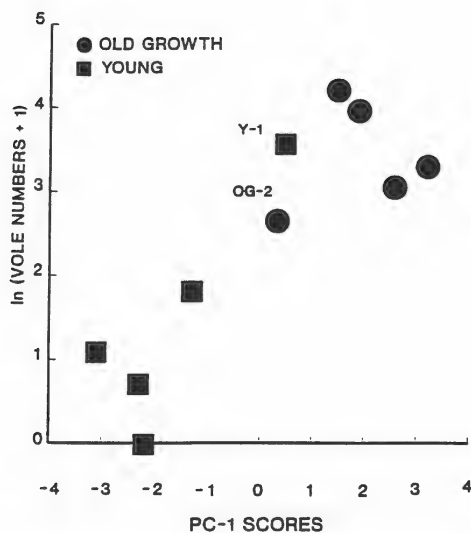


Figure 4. Relationship of the total number of individual voles captured (log transformed) during the 4 years (1988-1991) in each stand with the scores from the first principal component (PC-1). Y-1 and OG-2 are the young and old-growth stands, respectively, that had mean number of voles captured most different from the other stands within their respective stand age-class.

TABLE 1. Relationship (Pearson correlation coefficients, r) of habitat variables with the first 2 principal components.

Variable	Principal component 1		Principal component 2	
	r	P^1	r	P
Herb cover	0.33	0.3	-0.13	0.7
Fine woody debris cover	0.71	0.02	-0.57	0.08
Moss cover	0.47	0.17	0.59	0.07
Shrub cover	-0.13	0.7	0.90	0.0003
Organic soil depth	0.89	0.0006	0.11	0.76
Tree diameter CV ²	0.65	0.04	0.50	0.14
Large conifer trees	0.96	0.0001	0.06	0.86
Small conifer trees	-0.74	0.01	-0.51	0.13
Small deciduous trees	-0.65	0.04	0.42	0.23
Large snags	0.82	0.004	-0.37	0.29
Coarse woody debris	0.41	0.24	-0.004	0.99

¹Significance level.

²Coefficient of variation of diameter at breast height (dbh).

California red-backed voles may contribute significantly to dispersal of mycorrhizal fungi (Maser *et al.* 1978, Ure and Maser 1982, Hayes *et al.* 1986), and are included in the diet of many avian and mammalian carnivores (reviewed in Alexander and Verts 1992). Because of these relationships, their absence in forests may affect ecological processes. Retaining or managing for components of old-growth forests, such as deep organic-soil depths, residual large trees and snags, and coarse woody-debris (McComb *et al.* 1993) may make managed young stands more suitable for California red-backed voles.

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Reproductive Chronology of the Northern Flying Squirrel on the Olympic Peninsula, Washington

Abstract

The timing and frequency of breeding by northern flying squirrels (*Glaucomys sabrinus*) on the Olympic Peninsula, Washington were inferred from seasonal changes in the occurrence of juvenile flying squirrel remains in the pellets of northern spotted owls (*Strix occidentalis caurina*). Juvenile flying squirrels were uncommon or absent in the diet of spotted owls except during late August to early November. This suggested that breeding was largely concentrated in late May and early June, and that most females produced only a single litter in years when they bred. Infrequent breeding did occur outside the primary breeding season, as evidenced by the occasional occurrence of juvenile remains in pellets during mid-summer, late fall, and winter. Quantitative information on the population dynamics of flying squirrels and other arboreal mammals is important to our understanding of forest communities in the Pacific Northwest.

Introduction

Recent attempts to design management plans for spotted owls and late-successional forest ecosystems in the Pacific Northwest have been plagued by a considerable lack of knowledge regarding many species of animals and plants (Thomas *et al.* 1990, Forest Ecosystem Management Assessment Team 1993). This is particularly true of arboreal mammals like the flying squirrel and red tree vole (*Arborimus longicaudus*). Although these arboreal mammals are important prey for a variety of forest birds and mammals (Forsman *et al.* 1984, Barrows 1980) and play an important role in the spread of hyphogeous fungi within forest communities (Maser *et al.* 1978, Fogel and Trappe 1978), there is little information on their population dynamics or life history traits. As a result, their role in forest systems is only vaguely understood. Any attempt to understand processes and functions within forest communities must include a better understanding of the life histories and population dynamics of these little known mammals.

Because studies of arboreal mammals are labor-intensive and expensive, they are invariably limited to relatively small areas and there is always some

question regarding their applicability to larger geographic areas. In this paper we describe a study in which we used the seasonal occurrence of juvenile flying squirrel remains in pellets of spotted owls to estimate the timing and frequency of breeding by flying squirrels within a relatively large geographic region. The data were collected during a study of the habitat use and diet of spotted owls on the Olympic Peninsula in northwestern Washington. By examining flying squirrel remains in the pellets of owls, we were able to sample from the flying squirrel population throughout the year and to examine large numbers of squirrels from many different locations on the peninsula.

Study Area and Methods

The Olympic Peninsula is characterized by mountainous terrain covered by dense coniferous forests of western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*), and Douglas-fir (*Pseudotsuga menziesii*). Forests where we found spotted owls were typically dominated by multilayered canopies in which the dominant overstory trees exceeded 100 cm diameter at breast height (dbh). Some owls were also found in stands of younger, smaller trees (20-50 cm dbh) interspersed with scattered patches of large old trees. Our study area included the entire peninsula.

Pellets were collected from spotted owls between 1 March 1987 and 31 August 1989. During fall and winter (September-February), we collected pellets from 20 radio-marked adult owls by locating the owls in their roost trees and then

¹Current address: 138 W. Church Street, Evansville, Wisconsin 53536

²Current address: Arizona Department of Game and Fish, HC 62, Box 57201, Pine Top, Arizona 85935

³Current address: USDA Forest Service, Pacific Southwest Research Station, 1700 Bayview Drive, Arcata, California 95521

⁴Current address: USDA Forest Service, Targhee National Forest, P.O. Box 208, St. Anthony, Idaho 83445

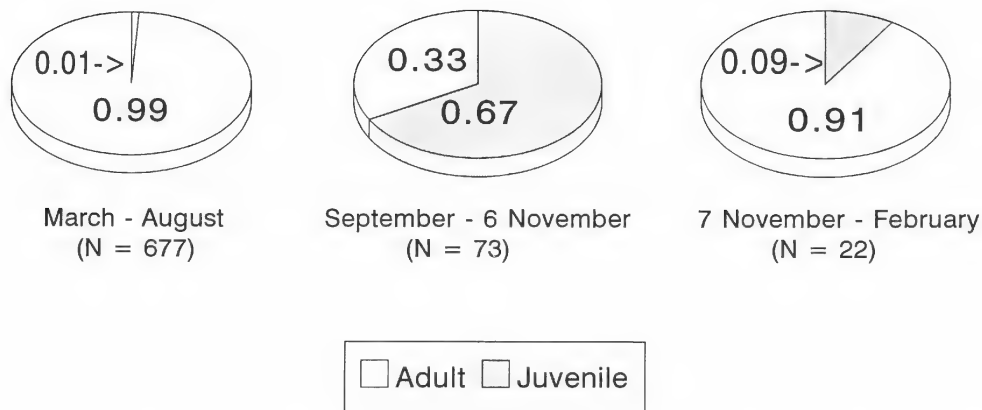


Figure 1. Relative proportions of juvenile and adult flying squirrels in the diet of spotted owls during different periods of the year on the Olympic Peninsula, Washington. Data summarized from March 1987-August 1989. Sample sizes indicate number of flying squirrels identified in pellets.

returning within a few days to see if a pellet had been regurgitated. In most cases, we could determine the exact date that pellets from radio-marked birds were regurgitated. During spring and summer (March-August), we continued to collect known-age pellets from radio-marked owls, and also collected many other pellets from owls that were not radio-marked. Pellets from owls that were not radio-marked usually could not be assigned to an exact date of regurgitation. Pellets in the latter category were collected from roosts that were cleared of pellets every 2-6 weeks. We assigned these pellets to seasonal categories based on the date collected and the previous date that the roost had been cleared. Because owls infrequently regurgitated pellets in their roosts during the fall and winter, the number of pellets collected during that period was much smaller than during spring and summer. Old, heavily weathered pellets were not included in seasonal analyses.

Flying squirrels were assigned to age categories based on size of skeletal parts, tooth development, and degree of fusion of epiphyseal cartilages. Very small individuals with unfused epiphyses and partially erupted molars were labeled as juveniles (generally less than 4 months old). Larger individuals with moderately to fully fused epiphyses and fully erupted molars were classified as adults. In cases where skulls were missing, age determination was based on the size of leg bones and degree of fusion of the epiphyses.

Results and Discussion

Skeletal remains of 772 flying squirrels were examined (712 adults, 60 juveniles). The occurrence of juvenile squirrels in the diet followed a distinct seasonal pattern (Figure 1). From early November to late August, juveniles comprised a very small proportion of the flying squirrels taken by owls. Between 1 September and 6 November, the proportion of juvenile flying squirrels in pellets increased dramatically (Figure 1). The initial flush of juveniles in early September was comprised almost entirely of very young animals, estimated to be 40-70 days old. Very young juveniles were largely absent in the sample until October and early November.

The marked increase of very small juvenile flying squirrels in the owl diet during a relatively brief period (September-October), and their relative absence in the diet during the rest of the year, indicated that breeding by flying squirrels on the Olympic Peninsula was largely concentrated in late May and early June. We arrived at this estimate by back-dating from the time when juvenile flying squirrels became common in the diet (1 September). To do this we assumed a gestation period of 37-40 days and a period of 40-50 days before juveniles began to explore outside their natal dens (Muul 1969).

The few juvenile flying squirrels captured by owls outside the September-October period indicated that breeding during late summer and early spring did occur, but was infrequent. The existence

of a single rather narrow birth pulse also suggested that, in years when they bred, most females produced only one litter.

A potential bias in using the diet of a predator to assess characteristics of a prey population is that the predator may not sample all cohorts randomly. We did not feel this was a concern in our analysis because we were interested only in the timing and frequency of breeding as indicated by seasonal changes in the occurrence of one cohort (juveniles). It would be inappropriate to draw conclusions about the age structure of the entire population from our data, as juvenile flying squirrels were probably much more susceptible to predation than adults.

Previous studies of the northern flying squirrel in Canada (Cowan 1936, Davis 1963) indicated that the peak breeding season was March and April, but pregnant females or litters have been reported from March to December (Dice and Sherman 1922, Grinnell and Storer 1924, Muul 1969, Raphael 1984, Seton 1929, Wells-Gosling and Heaney 1984, Witt 1991). Based on examination of 916 animals that were live-trapped and 176 animals that were necropsied, A. B. Carey (pers. comm.) concluded that the breeding season of northern flying squirrels in the southern Coastal Ranges of Oregon occurred during late April to mid-July, with a peak from late May to early June. Our observations, using a very different sampling technique, and in an area nearly 450 km north of Carey's study area, lead us to very similar conclusions regarding the reproductive chronology of the northern flying squirrel. The only substantial difference was that our observations indicated infrequent instances of breeding during late summer. Observations by Raphael (1984) and Witt (1991) also suggested occasional instances of breeding by northern flying squirrels during mid-summer or fall.

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- Studies by Cowan (1936) and Davis (1963) indicated a much earlier breeding season for the northern flying squirrel than in our study or in the studies by Witt (1991) and Carey (pers. comm.). Whether these differences were due to small sample size in the earlier studies or to real differences in timing of breeding is not clear. It could be that breeding is timed differently in different geographic areas, such that weaning occurs when food is most abundant. On the Olympic Peninsula, for example, young flying squirrels seem to be leaving the nest at about the same time that the fall bloom of hypogeous fungi occurs. Hypogeous fungi are a major source of food for northern flying squirrels in the Pacific Northwest (Maser *et al.* 1986, McKeever 1960), and reach peak productivity in late spring and fall (Fogel 1976).
- Historically, most studies of owl diets have produced lists of prey found in pellets, but have paid little attention to the age structure of the prey animals captured. As our analysis indicates, data on the age structure of prey in owl pellets can provide interesting insights into the biology and behavior of both predator and prey. These sorts of insights are possible, however, only if pellets are collected at relatively frequent intervals so that dates of capture can be approximated.

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Identification of *Sorex monticolus* and *Sorex vagrans* from British Columbia

Abstract

Sorex monticolus and *Sorex vagrans* usually are identified by use of tine characters of the upper incisors. Because not all specimens are clearly identifiable by tine characters, I used four cranial measurements thought to be useful characters by those familiar with the genus *Sorex*. Univariate and bivariate comparisons did not yield reliable methods of discrimination. Discriminant analysis permitted identification of many of the unidentified specimens.

A comparison of qualitative tine character states in members of the two species groups in British Columbia, as identified by discriminant analysis, provided no universal differences in these characters. Using the position of the medial tine relative to pigment levels is still the best means of discriminating between these two species of *Sorex*. Final curation of the collection suggested the level of pigment and size of tine on the upper first incisor were the two characters that varied most consistently with identifications of the two species determined by discriminant analysis. Use of discriminant analysis has proven helpful when attempting to identify other taxa of mammals when key characters are confusing or missing.

Introduction

The identification of *Sorex vagrans* and *S. monticolus* is problematic (Hennings and Hoffmann 1977; Junge and Hoffmann 1981; van Zyll de Jong 1983; Carraway 1990). The first upper incisors (I1) of these shrews possess a tine or accessory cusp on the medial edge. A combination of the size of the tine relative to the size of the I1, the level and amount of pigment on the tine, and whether a gap occurs between the pigment of the main body of the I1 and the tine are characters that have been used to separate specimens of the two species. Hennings and Hoffmann (1977:9) described *Sorex vagrans* as having "medial tines on [the] first upper incisor situated at approximately the upper edge of the pigment; set off distinctly by a gap in color." In *Sorex monticolus* the "tines are larger, the pigment darker, and the incisors more robust than those of *vagrans*" (Hennings and Hoffmann 1977:14). Illustrations in Hennings and Hoffmann (1977) show that no gap in color is present in *Sorex monticolus*. Although these tine characters often are useful in separating the species, many specimens are intermediate or mixed in character, or are missing key characters due to tooth wear or tooth loss.

Bogan (1977) and Choate (1973) have shown that very similar species can be identified by use of simple morphometric measurements in discriminant analysis. In this study, a small suite of morphometric characters was sought that might permit identification of unidentified shrew specimens (unknowns) by discriminant analysis.

The presence of age variation (Jackson 1928; Rudd 1955), the absence of sexual variation (Rudd 1955), and the presence of size variation that does not follow Bergmann's Rule (Hennings and Hoffmann 1977) have been reported in shrews. These sources of variation were assessed for the sample of specimens in this study to determine whether they might significantly affect a discriminant analysis.

Methods and Materials

Specimens identified as *Sorex monticolus* (including *S. obscurus*) and *S. vagrans*, housed in the Mammalogy collection at the Royal Ontario Museum (ROM), required updated identification. Use of tine characters as described in existing keys (Hennings and Hoffman 1977; van Zyll de Jong 1983) permitted the conclusive identification of 143 of 244 specimens (59%) from British Columbia, referred to hereafter as knowns.

Four characters were used in discriminant analyses to identify as many unknown specimens as possible. The characters were least interorbital breadth and palatal length described by Hennings and Hoffmann (1977), and width across first upper incisors and width across fourth upper unicuspid suggested by Sarah George (personal communication). Two other characters suggested, respectively, by the aforementioned were not suitable for this analysis. Width across the molars was dropped because it showed significant age variation and its inclusion would have severely limited

sample sizes in discriminant analyses. Sixteen percent of the time condylobasal length could not be measured because of crushed or misshapen braincases. To maximize the number of specimens that might be identified using quantitative methods condylobasal length was removed from analyses. For this reason, the trivariate method of identifying *S. vagrans* and *S. monticolus* described in Hennings and Hoffmann (1977) was not attempted.

Skin characters were not used because shrew skins are prone to rapid degradation in the field and standard external measurements are prone to measuring error. Dried specimens do not permit reliable friction pad or digital callosity counts (van Zyll de Jong 1983).

Characters were measured using a Wild Heerbrugg dissecting microscope furnished with a 120 gradation ocular micrometer. Reported measurements are given in millimetres.

The museum specimens used in this study were assumed to be representative of the populations sampled. All analyses were considered significant at the 5% level.

Analysis of variance (ANOVA), multivariate analysis of variance (MANOVA), and Tukey's studentized range test analyses were performed using the GLM procedure in Statistical Analysis System (SAS Institute Inc. 1985). Because of limited sample sizes, multiple range tests could not be performed to more fully explore variation associated with age, sex, and/or species.

All specimens were aged by use of Rudd's (1955) age categories based on tooth-wear characters of the upper third premolar and upper three molars. The three gradations within each numbered category (e.g., -2, 2, and +2) of Rudd's tooth-wear descriptions were pooled to increase sample sizes.

Variation attributable to sex was tested in both age class 3 of *S. vagrans* and age class 2 of *S. monticolus*. Specimens were taken from a single age class to minimize the influence of age. Sexual variation was significant in the sample of *S. vagrans*, but was not significant in *S. monticolus*.

I used a simplified approach to search for some indication of geographic variation in *S. monticolus*. Three subsets were defined based on latitude: 49° 00' to 52° 59' = southern group; 53° 00' to 54° 59' = central group; and 55° 00' to 60° 00' = northern group.

A multi-group discriminant analysis was done using BIOSTAT II (Pimentel and Smith 1986) with the five groupings warranted by the results of ANOVA and MANOVA. The sexes in *S. vagrans* were separated into two groups in the multi-group discriminant analysis. Significant differences between the geographically-defined subsets led to three groups of *S. monticolus* in the multi-group discriminant analysis. Data from all localities were pooled for *S. vagrans* because all were from southern latitudes.

To develop a quantitative method to identify unknowns, a second discriminant analysis (DISCRIMINANT) was run using Statistical Procedures for the Social Sciences (SPSSX 1986). All discriminant analyses were run assuming equal group priors. The groups defined for the multi-group discriminant analysis were pooled for the two-group discriminant analysis. The two groups represented each species sample. The resulting unstandardized coefficients and constant of the two-group discriminant analysis permit the identification of unknown specimens from British Columbia (Choate 1973; Bogan 1974).

After surveying a number of specimens from both species groups, easily discernible gradations in characters became evident. Five tine characters were recorded:

1. Tine size was scored as small (1), medium (2), or large (3).
2. Tine pigment was scored as none (1), light (2), medium (3), or dark (4).
3. Pigment gap was scored as obvious (1), vague (2), or absent (3).
4. Tooth pigment was scored as pale (1), medium (2), or dark (3).
5. Pigment level relative to the tine was scored as below (1), at (2), mid-way up (3), or above (4) the tine.

Although subjective in nature, I found these character states discrete enough to be reliably assigned to all specimens. The percentage occurrence of the different tine states was tabulated for all specimens identified as *S. monticolus* or *S. vagrans* by discriminant analysis to ascertain differences between the two species. The specimens included all knowns (clear tine characters) and all unknowns (mixed or missing tine characters) diagnosed by discriminant analysis. The intent of this exercise was to determine whether a subset of the five characters would be sufficient to clearly discriminate between the two species.

TABLE 1. F-Test and Tukey studentized range test results for subsets of *Sorex* measurements to determine the affect of sex and geographic areas on skull characters.

Character and variable	Sex Comparison		Geographic Area Central=C, North=N, and South=S
	<i>S. vagrans</i> Age class 3 (n = 22)	<i>S. monticolus</i> Age class 2 (n = 21)	<i>S. monticolus</i> Age class 2 (n = 20)
Least Interorbital Breadth			
F	13.20	0.42	3.17
p	0.002	0.53	0.07
Tukey			C N S
Palatal Length			
F	18.30	0.19	7.23
p	0.0004	0.67	0.005
Tukey			C N S
Width across First Upper Incisors			
F	1.45	6.32	7.60
p	0.24	0.02	0.004
Tukey			C N S
Width across Fourth Upper Unicuspid			
F	3.03	0.15	5.87
p	0.10	0.70	0.01
Tukey			C N S
MANOVA			
F	5.41	2.33	2.87-4.23
p	0.005	0.10	0.01-0.02

Results

The sexes of *S. vagrans* significantly differed for least interorbital breadth and palatal length (Table 1). Females were relatively larger than males for all four characters in *S. vagrans*. MANOVA also showed a significant difference between the two sexes (Table 1).

The sexes of *S. monticolus* showed significant differences in width across first upper incisors, although the MANOVA did not support this difference between the two sexes (Table 1). Males were larger than females for width across first upper incisors.

The three groups used to assess age variation included 14 female *S. monticolus* from the northern region (age classes 1-3), 20 male *S. monticolus* from the central region (age classes 1-3), and

20 male *S. vagrans* from the southern region (age classes 2-4). None of the three samples showed significant differences between age classes for least interorbital breadth, palatal length, width across first upper incisors, or width across fourth upper unicuspid. Width across the upper molars showed significant age variation in the male *S. monticolus* from the central region, thus, this character was not included in this study.

Palatal length, width across first upper incisors, and width across fourth upper unicuspid were significantly different between the three geographic samples of *S. monticolus* (Table 1). These differences are present at the univariate and multivariate levels of analysis.

None of the means of single characters are distinct among groups or between species (Table 2). Bivariate plots were made of all six of the

TABLE 2. Univariate statistics for four variables of *Sorex vagrans* and *S. monticolus*. The five samples include central, northern, and southern groups of *S. monticolus* and female and male groups of *S. vagrans*.

<i>Sorex monticolus</i> (males, age class 2)				
Character Measured (mm)	Geographic Region			Range
	Central (n = 4) $\bar{X} \pm 2 \text{ SD}$	Northern (n = 9) $\bar{X} \pm 2 \text{ SD}$	Southern (n = 7) $\bar{X} \pm 2 \text{ SD}$	
Least Interorbital Breadth	3.74 $\pm$.32	3.70 $\pm$.20	3.62 $\pm$.28	3.2-4.0
Palatal Length	7.59 $\pm$.64	7.28 $\pm$.28	7.35 $\pm$.44	6.6-8.1
Width across Upper Incisors	1.48 $\pm$.24	1.47 $\pm$.18	1.48 $\pm$.30	1.3-1.9
Width across Upper Fourth Unicuspid	2.37 $\pm$.34	2.38 $\pm$.14	2.33 $\pm$.22	2.1-2.6
<i>Sorex vagrans</i> (south region, age class 3)				
Character Measured (mm)	Sex		Range	
	Female (n = 8) $\bar{X} \pm 2 \text{ SD}$	Male (n = 14) $\bar{X} \pm 2 \text{ SD}$		
Least Interorbital Breadth	3.53 $\pm$.32	3.32 $\pm$.24	3.2-3.8	
Palatal Length	6.96 $\pm$.50	6.60 $\pm$.36	6.3-7.3	
Width across Upper Incisors	1.38 $\pm$.14	1.33 $\pm$.14	1.2-1.5	
Width across Upper Fourth Unicuspid	2.16 $\pm$.22	2.06 $\pm$.20	1.9-2.3	

measurement pairs. None of the pairs showed separation sufficient to confidently identify specimens using this technique.

The classification of unknowns by the multi-group discriminant analysis and the two-group discriminant analysis were virtually identical. Two of six specimens misclassified in the two-group discriminant analysis differed from those misclassified in the multi-group discriminant analysis. In the two-group analysis three *S. monticolus* and three *S. vagrans* were misclassified. All three specimens of known *S. vagrans* that were misclassified were females (Figure 1).

By measuring four skull characters, calculating a discriminant function score for the first canonical variate, and plotting the score on Figure 1, over 90% of the specimens in this study were easily identified as a member of one of the two species groups. The equation to calculate the discriminant function score is:

$$X = 2.011757(\text{least interorbital breadth}) + 2.246716(\text{palatal length}) - 0.832296(\text{width across first upper incisors}) + 3.848037(\text{width across fourth upper unicuspid}) - 30.97091,$$

where X is the discriminant score, the first four numeric values are the unstandardized discriminant coefficients, the fifth value is the constant, and the character names represent the values

of the respective characters measured on each specimen. Characters should be measured by use of a dissecting microscope with an ocular micrometer because small errors in measurement can have a substantial effect on the calculated discriminant score (Choate 1973). The constants in the above equation double and quadruple measurement errors. Furthermore, the size and delicacy of the shrew skull virtually prohibit accurate measurement using calipers or without some means of magnification.

The two-group discriminant analysis provides a practical method to identify unknown specimens. The stacked histogram (Figure 1) shows some overlap among members of the two species in the discriminant function 1 scores. Specimens with discriminant scores greater than -0.6131 were identified as *S. monticolus*, while those with values less than -0.7721 were identified as *S. vagrans*. Specimens with discriminant scores between these values were misidentified, as were two extreme outliers.

The qualitative characters of *S. monticolus* (Table 3) tend toward the high character state for all five characters (more than 80% of specimens exhibiting characters at level 3 or more for all characters except tooth pigment). *S. vagrans* show a broad range of character states for virtually all of the characters. More than 90% of specimens exhibit

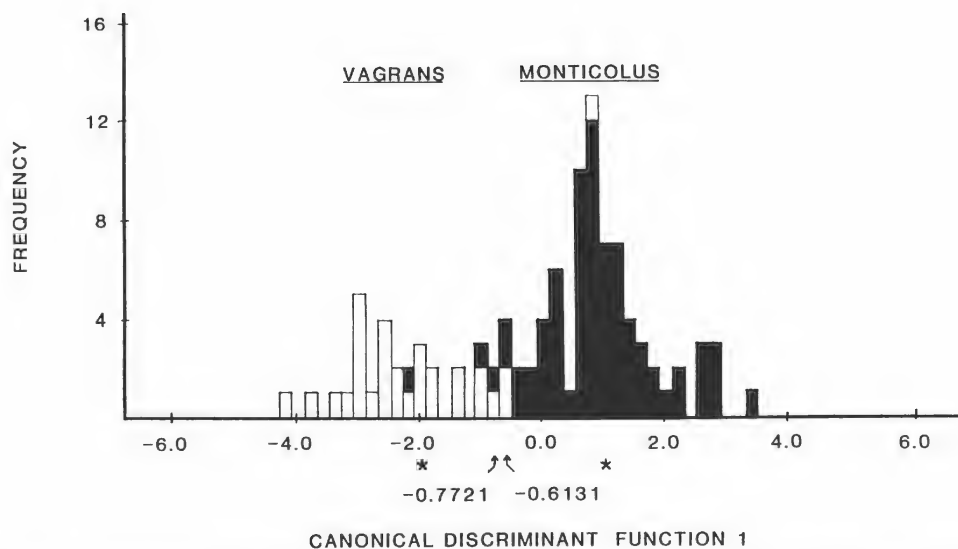


Figure 1. Stacked histogram of *S. vagrans* and *S. monticolus* canonical discriminant function 1 scores. Group centroids are marked by an asterisk. Arrows mark the discriminant scores that represent the maximal discriminant score that will reliably identify a *S. vagrans* (left arrow) and the minimal discriminant score that will reliably identify a *S. monticolus* (right arrow).

TABLE 3. Summary of qualitative tine characters exhibited by specimens as identified by multi-group discriminant analysis. Percentage is calculated from the sum of scored individuals for each species and character.

Character State		Character									
		Tine n	Size %	Tine n	Pigment %	Gap n	Clarity %	Tooth n	Pigment %	Pigment n	Level %
<i>Sorex monticolus</i>	1	7	7	1	1	2	2	6	6	2	2
	2	8	8	13	13	11	11	73	75	5	5
	3	82	85	75	76	84	87	18	19	8	8
	4	0	0	9	9	0	0	0	0	84	85
	Unscored	5		4		5			5		3
<i>Sorex vagrans</i>	1	35	42	4	5	32	39	18	22	21	25
	2	31	37	40	48	42	51	63	76	31	37
	3	17	20	37	45	8	10	2	2	26	31
	4	0	0	2	2	0	0	0	0	6	7
	Unscored	6		6		7		6		5	

character states ranging from 1 to 3. For each of the five qualitative characters, more than 20% of the *S. vagrans* specimens appear in two or more separate character states. There is no clear distinction between the characters or combination of characters associated with the incisors that clearly distinguish all *S. monticolus* from all *S. vagrans*.

Discussion

Rudd (1955) maintained that sexual variation had no significant affect on cranial morphology, and others (Carraway 1990) have made similar assumptions in their work. In this study, *S. vagrans* showed significant sexual variation for least

interorbital breadth and palatal length (Table 1). Carraway (personal communication) believes that the sex of about 10% of all *Sorex* found in museum collections is misidentified. If the specimens housed at the ROM follow this generality, the sexual variation in this sample may be even more significant than this analysis suggests. This significant sexual variation and the resulting significant multivariate effect for Rudd age category 3 suggests that data should be examined for dimorphism.

Although many others have reported age variation in shrews (Jackson 1928; Rudd 1955), only width across upper molars showed any significant difference among age categories. There was no statistical difference at the multivariate level for the four characters used in this study. Admittedly, the sample sizes are small. The results do, however, suggest that age variation should be routinely explored before assuming any significance.

Although the significant groupings resulting from Tukey's studentized range test vary from character to character, the measurements for the central group are consistently the largest, whereas those of the southern sample are the smallest (Table 1). Although there is no evidence of Bergmann's Rule (Smith 1980), coastal versus inland location, elevational differences, rainshadow effects, or other parameters may be correlated with the morphological differences exhibited in the specimens examined. A larger sample size, preferably of a single subspecies, is necessary to further explore the possible factors correlated with morphological variation.

The classifications of the two-group and multi-group discriminant analysis differed for only six specimens. It is not surprising that the three differently classified *S. vagrans* in the two-group discriminant analysis were females; the larger female *S. vagrans* are more likely to be classified as *S. monticolus* than are the smaller males. The three differently classified *S. monticolus* clearly exhibited *monticolus* key characters.

The use of discriminant scores for the first canonical variate has proven useful in identifying mouse and bat species that exhibit confusing key characters (Choate 1973; Bogan 1974). Despite significant multivariate differences in sex and geographic groupings, the classification results of the

multi-group and two-group discriminant analyses were identical in rate of successful classification of the known specimens.

Those specimens whose discriminant score values are between -0.7721 and -0.6131 should be considered *S. vagrans* ? or *S. monticolus* ?, rather than as *Sorex* sp. *S. vagrans* and *S. monticolus* are readily distinguished from other *Sorex* species by shared dental characters (van Zyll de Jong 1983). By assigning a question mark to a tentative identification, a higher level of systematic information is retained in the museum collection.

The characters described by Hennings and Hoffmann (1977) may be individually striking when examining specimens of *S. vagrans* or *S. monticolus*. When originally examining specimens, I found concentrating on the darkness of the pigment, and the presence or absence of a break in the pigment between the tine and the main body of the incisor confused identification decisions. While performing final curation after completion of the analyses described here, I found that the level of pigment on the main body of the I1 and the size of the tine were the two characters that seemed to vary most consistently with discriminant analysis diagnoses. Concentrating only on the variation between these two characters greatly simplified identification decisions.

Distinctive tine characters led to the prompt identification of *S. monticolus* and *S. vagrans* 60% of the time. When tine characters were absent or became mixed in nature, the use of four easily measured cranial characters and the results of a discriminant analysis permitted the identification of a further 35% of the shrews awaiting curation. For collections lacking large series of specimens, a quantitative identification tool for the cranial material of these two very confusing species provides a means of assigning specific nomenclature to museum specimens.

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Appendix I

Sorex monticolus.—

British Columbia. (n = 75) Alta Lake (1); Bennett (1); Chezacut Lake, Chilcotin, Range 3 (1); Cultus Lake (2); First subalpine *Betula* community near Ray's Road, 59° 51' N, 136° 40' W (4); Glacier (4); Golden (1); Hope-Princeton Highway (1); Lakelse Lake, Range 5 (4); Manning Park (3); McClinton Creek, Graham Island (1); Mount Revelstoke (3); Mount Revelstoke National Park (1); North Vancouver (2); Nulki Lake, Range 4 (5); Point Grey (2); Repeat alpine moist grass community N Den Site D, 59° 40' N, 136° 31' W (1); Repeat alpine *Salix* community N Den Site D, 59° 40' N, 136° 31' W (3); Repeat subalpine *Salix* community at Den Stream, 59° 48' N, 136° 37' W (12); *Salix* experimental Den Site D, 59° 40' N, 135° 31' W (1); Seal Cove, Prince Rupert (5); Second alpine grass community S Den Site D, 59° 40' N, 136° 31' W (2); Second alpine roadside community at Den Site D, 59° 40' N, 136° 31' W (2); Second alpine *Salix* community S Den Site D, 59° 40' N, 136° 31' W (5); Second subalpine *Salix* community in F-08's typical area, 59° 40' N, 135° 31' W (1); Sixteen Mile Lake, Quesnel (3); Vancouver (1); Vermillion Crossing (3).

Sorex vagrans.—

British Columbia. (n = 30) Bolean Lake, 7 mi. NE Falkland (1); Cameron Lake, Vancouver Island (1);

Coldstream, Okanagan (4); Cowichan Lake, Vancouver Island (1); Duncan, Vancouver Island (2); Goldstream (1); Huntingdon (3); Mount Revelstoke (1); Mount Revelstoke National Park (3); Okanagan Landing (5); Point Grey (3); Quatsino (1); Sugar Lake (1); Vancouver (1); Vernon (2).

Unknowns.—

British Columbia. (n = 86) Balsam Lake (1); Beaver Pit, Glacier National Park (1); Beaver River, Glacier National Park (1); Bolean Lake, 7 mi. NE Falkland (1); Cameron Lake, Vancouver Island (3); Coldstream, Okanagan (3); Cranbrook (3); Creston (3); Cultus Lake, Okanagan (1); Departure Bay (1); Duncan, Vancouver Island (1); Eagle Bay, Shuswap Lake (1); Field (1); First alpine *Salix* community, near Nadahini River, 59° 41' N, 136° 33' W (1); Glacier (3); Goldstream, Vancouver Island (1); near Haines Road (3); Huntingdon (1); Lakelse Lake (3); Lulu Island (3); Manning Park (2); McClinton Creek, Graham Island (4); McClinton Creek, Masset Inlet (1); Mount Coakley, Vancouver Island (2); Mount Revelstoke (1); Mount Revelstoke National Park (14); No locality (2); Okanagan Landing (2); Point Grey (2); Seal Cove, Prince Rupert (4); Silver Star Mountain, 12 mi. NE Vernon (1); Sixteen Mile Lake (5); Sooke (1); Sugar Lake (3); Summit Lake (1); Vancouver (3); Wynndel (2).

and

A. Scott Feldhausen, Bureau of Land Management, P.O. Box 430, Salmon, Idaho 83467

Juvenile Salmonid Densities and Habitat Use in the Main-stem Situk River, Alaska, and Potential Effects of Glacial Flooding

Abstract

Densities and habitat use of juvenile coho salmon (*Oncorhynchus kisutch*), sockeye salmon (*O. nerka*), steelhead (*O. mykiss*), and Dolly Varden (*Salvelinus malma*) were determined in the main-stem Situk River, Alaska. Three habitat types (channel edges, willow edges, and debris pools) were sampled at two downstream sites (lower river) and at two upstream sites (upper river) biweekly from May to September and once in November 1989. For most species, fry (age 0) most often used channel edges with little cover, whereas parr (age ≥ 1) almost exclusively occupied willow edges and debris pools. Within the same habitat types, densities were significantly greater for most species and life-history stages in the upper than in the lower river; steelhead parr, with densities similar in like habitats in the upper and lower river, were a notable exception. Peak fry densities (fish/100 m²) were 2,331 coho, 155 steelhead, and 14 sockeye, whereas peak parr densities were 281 coho, 82 steelhead, and 44 Dolly Varden. Mean length of fry and parr of all species was greater in the lower river than in the upper river. With baseline information from this study, fisheries managers can identify strategies to restore fish and habitat that could be impacted by flooding in the Situk River. Hubbard Glacier is expected to advance and dam Russell Fiord by the year 2000, and overflow from the fiord will flood the Situk River, drastically altering fish rearing habitat.

Introduction

Fisheries of the Situk River in Southeast Alaska will be altered when the Hubbard Glacier advances and dams Russell Fiord, because overflow from the resulting "Russell Lake" will flood the river (Figure 1) (Clark and Paustian 1989). Closure of Russell Fiord by Hubbard Glacier is probable by the year 2000 (Trabant *et al.* 1991). Damming of Russell Fiord and flooding of the Situk River occurred most recently in the mid-1800s (de Laguna *et al.* 1964). The Situk River currently supports commercial, sport, and subsistence fisheries for Pacific salmonids valued at \$2-3 million annually. Knowledge of the life history and habitat use of juvenile salmonids in the main-stem Situk River is essential to predict effects of flooding on rearing salmonids.

Limited life-history information is available on juvenile coho salmon (*Oncorhynchus kisutch*), sockeye salmon (*O. nerka*), steelhead (*O. mykiss*), and Dolly Varden (*Salvelinus malma*) in the Situk River. Downstream migrants have been enumerated from Old Situk River, a major tributary of the Situk River (Figure 1) (Thedinga *et al.* 1991). Migration timing, size, and salinity tolerance of

juvenile sockeye in the Situk River estuary were examined by Heifetz *et al.* (1989). Extensive life history information on juvenile chinook salmon (*O. tshawytscha*) in the Situk River has been described by Johnson *et al.* (1992).

Our objectives were to examine densities and habitat use of juvenile coho and sockeye salmon, steelhead, and Dolly Varden in the Situk River and to predict some of the potential effects of flooding on fish populations and rearing habitat. This baseline information will enable fisheries managers to identify strategies to restore fish and habitat that could later be impacted by flooding.

Study Area

The Situk River, 18 km southeast of Yakutat, Alaska (Figure 1), is a clear, fourth-order, coastal stream that contains stocks of five Pacific salmon (*Oncorhynchus* spp.), steelhead, cutthroat trout (*O. clarki*), and Dolly Varden. The main stem is 35 km long from the outlet of Situk Lake (315 ha) to the ocean. Average summer flow is approximately 6 m³/s (Clark and Paustian 1989). Tides twice daily influence the lower 3.5 km of the Situk River before it enters the estuary. At high tide the lower portion of the river, referred to as lower river, deepens, water velocity subsides, and salinity increases but remains low (mean bottom salinity

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

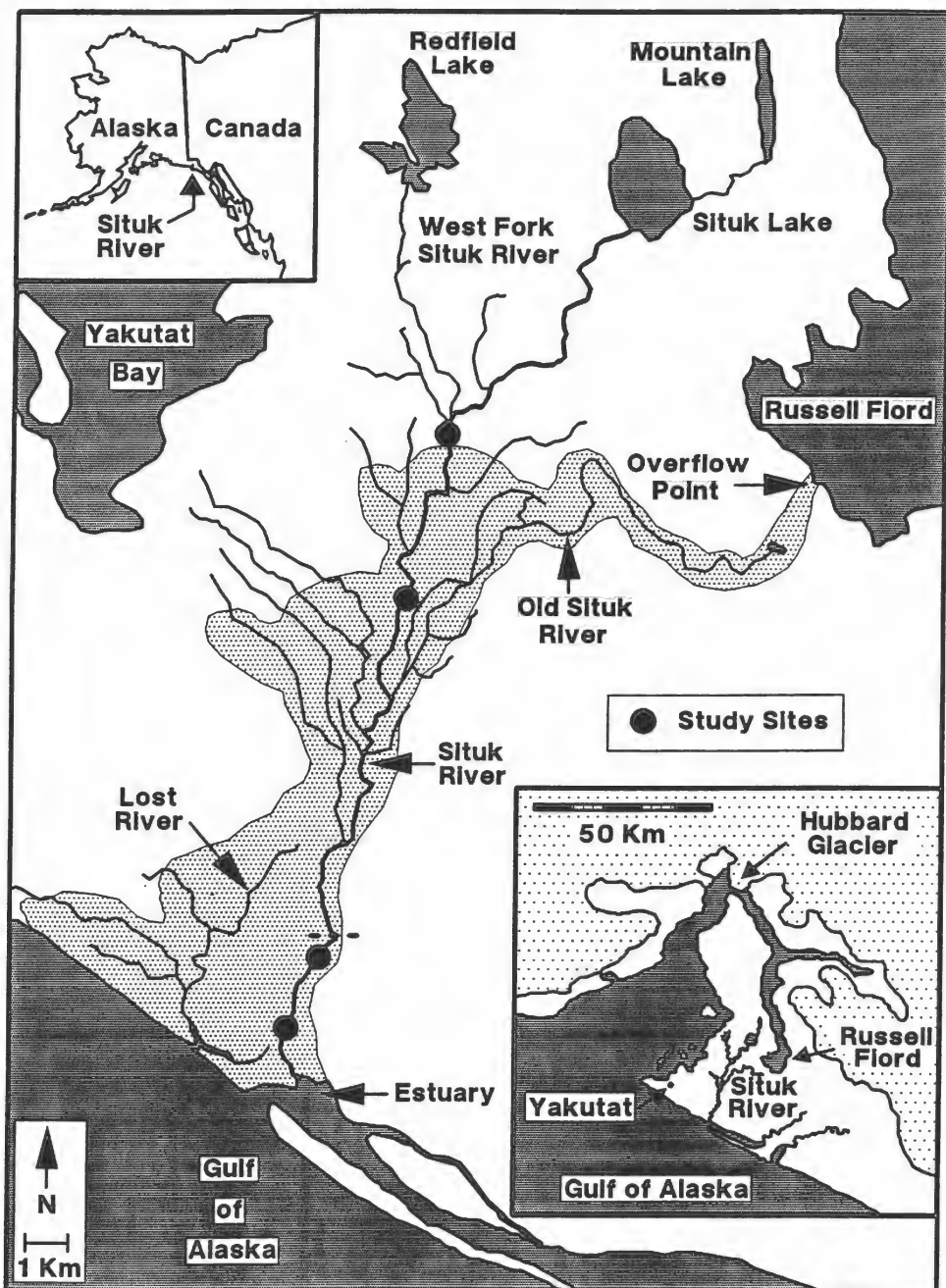


Figure 1. Sites sampled for juvenile salmonids in the main-stem Situk River, Alaska, 1989. Stippled area on main stem represents predicted flood zone. Dashed line across main stem represents upper boundary of tidal influence and also separates upper river from lower river. In lower inset, arrow from Hubbard Glacier points to location of potential ice dam.

$<5.0^{(0/00)}$ (Heifetz *et al.* 1989). The remainder of the main stem is not affected by tides and is considered the upper river. The river has two major third-order tributaries: Old Situk River is 20 km long, originates at a small pond, and has an average summer flow of $1.5 \text{ m}^3/\text{s}$ (Thedinga *et al.* 1991); and West Fork Situk River is 10 km long, flows out of Redfield Lake (200 ha), and has an average summer flow of about $1 \text{ m}^3/\text{s}$.

Methods

We sampled two sites in the lower river and two sites in the upper river (Figure 1) biweekly from 10 May to 22 September 1989 to estimate fish density and habitat use. These sites were sampled again on 30 November 1989 for relative abundance and late fall distribution, but we did not estimate fish density. Sites were selected based on similarity of habitats (i.e., like habitats existed among all sites) and ease of accessibility. Except in November, we sampled three principal habitat types at each site: three channel edges (main-channel edge with little or no overhanging vegetation); one willow edge (main-channel edge with dense overhanging willow (*Salix* sp.) or other vegetation and submerged roots); and one debris pool (pool containing large woody debris—pieces $\geq 10 \text{ cm}$ diameter and 1 m long). Other habitat in the main stem was mostly main-channel thalweg, probably little utilized by rearing salmonids (Murphy *et al.* 1989). In November we sampled only willow edges and debris pools.

Fish were caught in the different habitats with either seines or minnow traps. Fish in channel edges were caught with a pole seine (5.4 m long, 1.5 m deep, and 6-mm mesh) pulled against the current parallel to shore for 20 m (area seined = 74 m^2). Seines could not be used in willow edges or debris pools because they snagged on submerged roots and large woody debris (LWD). In willow edges and debris pools, fish were caught with minnow traps (spaced 3 m apart) baited with salmon roe; 7 traps were set in a 21-m section of willow edge and up to 15 traps were set in debris pools (area of pools was larger than willow edges and required more traps to saturate available habitat). All traps were set during the day.

We used the removal method (Zippin 1958) to estimate fish populations within habitat types. Three passes with a seine were usually made per channel edge; if no fish were caught in the first

pass, no further seining was done. In willow edges and debris pools, traps were set for 40 min, retrieved, emptied of fish, rebaited, and set again in the same location for 40 min. Traps were set at least three times. If the catch on the third set was not substantially reduced from the second set, additional sets were made until catch was reduced from the previous set. Fish caught in each seine or trap set were kept in separate containers. Immigration and emigration were assumed to be negligible during sampling. We placed the first minnow trap 3 m upstream from the lower boundary of willow edges and debris pools to limit attracting fish from downstream areas. Total catch was used in the analysis instead of the estimated $\hat{N}$ if the estimated probability of catch $\hat{q}$ was ≤ 0.20 . Fish density in each habitat type was computed by dividing the population estimate by the area seined or trapped. In November, minnow traps were set once in willow edges and debris pools and retrieved after 24 h.

Amount of available habitat was measured at each habitat type at each site during low flow and in the lower river at low tide. Linear transects perpendicular to streamflow were established at 3-m intervals in each habitat type. Total area of willow edges and of debris pools was estimated by multiplying mean width (measured at transects) by total length of habitat. For willow edges, area was based on the distance willow vegetation protruded over the river; for debris pools, area was based on the length and width of the part of the pool containing LWD. Water depth was measured at one-quarter, one-half, and three-quarters of the distance across each transect of each habitat type. Water velocity was measured at one-quarter, one-half, and three-quarters of the distance across the lower, middle, and upper transect of each habitat type. Total pieces of LWD were counted in each habitat type. In the lower river, water temperature was measured every 2 h with a continuous recording Endeco® thermograph from June through November 1989. In the upper river, water temperature was measured with a Datapod® at a U.S. Geological Survey gauging station about 1 km downstream from the confluence with West Fork Situk River. A more detailed description of habitat characteristics has been provided by Johnson *et al.* (1992).

Each sampling period, all sockeye, steelhead, and Dolly Varden, and a subsample of coho (minimum 100 fish) caught at each site were measured

for fork length (FL), and scale samples were taken from up to 25 fish of each species to determine age, except Dolly Varden, which have scales too small and difficult to remove. In this report, fry are fish that had reared less than a year in fresh water (age 0), whereas parr had reared one or more years in fresh water (age ≥ 1). Because assessment of rearing fish and habitat was the primary objective, smolts were omitted from analyses.

Vulnerability to capture in seines or minnow traps was assumed equal for most species and life-history stages. Exceptions were Dolly Varden fry and sockeye. Because few Dolly Varden fry were caught, they were omitted from analyses. Small size of fry and use of substrate interstices probably made Dolly Varden less vulnerable to capture than other fry. Few sockeye fry and no sockeye parr were caught in willow edges or debris pools, probably because they are primarily zooplankton feeders and thus not attracted to the bait (salmon roe) inside the minnow traps. For all other species and life stages, however, it was assumed that we were effectively removing most fish in all three habitat types, regardless of method of capture.

Within the upper and lower river sites, differences in mean fish densities by habitat type were examined by Friedman's tests (Zar 1974); sampling periods served as blocks and habitat types as treatments. Differences in mean fish densities between the same habitat types in the upper and lower river sites were examined by Mann-Whitney tests (Zar 1974); in like habitats, mean densities were compared between the upper and lower river for fry and parr of each species. Differences in mean fork length of each species and life stage between the upper and lower river sites (all sampling periods and habitat types combined) were examined by t-tests (Zar 1974).

Results

Habitat Characteristics

Water depth, velocity, and cover differed among habitat types. Average depth was greatest in debris pools (1.2 m) and least in channel edges (0.3 m). Average water velocity was greatest in willow edges (15 cm/s) and least in debris pools (10 cm/s). Cover was scarce in channel edges but was abundant in debris pools as LWD (range = 8-25 pieces) and in willow edges as overhanging vegetation and submerged roots.

Mean daily water temperature at the upper and lower river sites ranged between 9 and 15°C from

early June to September and peaked in mid-July. Summer water temperatures were consistently 1-2°C warmer in the upper river than in the lower river, probably because of the warming influence of Situk Lake. Water temperature dropped to 1.0-2.0°C by late November.

Life-History Stage

Fry dominated the catch during most sampling periods at both the upper river and lower river sites (Figure 2). All sockeye were fry, but nearly all Dolly Varden were parr. Coho parr dominated the catch (60%) only in debris pools in the lower river in May. All steelhead were parr in May and June and 54-99% fry thereafter, as fry emerged from the gravel beginning in July. Coho fry were caught from May through November, most sockeye fry from May through July, and steelhead fry from late July through November. Coho, steelhead, and Dolly Varden parr were caught from May to November.

Fry Densities and Habitat Use

Mean density (fish/100 m²) of coho fry differed significantly ($P < 0.05$) among habitat types at the lower river sites but was similar ($P > 0.05$) among habitats at the upper river sites (Figure 3). Lower river mean densities were greater in willow edges (range = 0-471) and debris pools (0-382) than in channel edges (0-82). In the upper river, mean densities ranged from 2 to over 1,400 coho in all habitat types. Fry density peaked earlier (May and June) in channel edges than in willow edges or debris pools (July). After July, coho fry density declined steadily at both the upper and lower river sites.

Mean density of steelhead fry did not differ significantly ($P > 0.05$) among habitat types at either the upper or the lower river sites; however, most sockeye fry were caught in channel edges. Sockeye (data not shown) and steelhead (Figure 3) fry densities peaked in late May and late July, respectively, in channel edges at both the upper and the lower river sites.

Within the same habitat types, mean densities (fish/100 m²) of coho and steelhead fry were significantly ($P < 0.10$) greater at the upper than at the lower river sites (Figure 3), whereas sockeye fry densities (data not shown) were similar ($P > 0.10$). Peak fry densities were 2,331 coho,

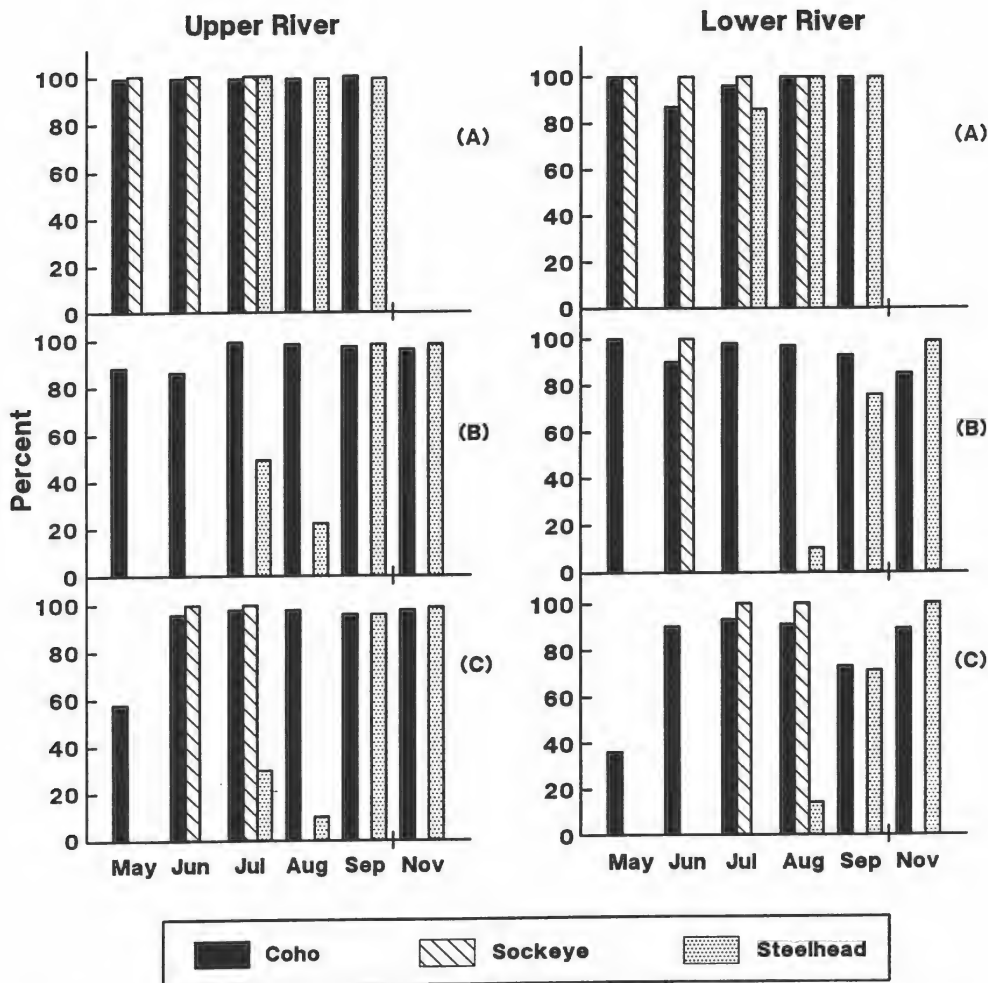


Figure 2. Percentage of fry (age 0) by habitat type in the upper and lower Situk River, Alaska, 1989. Dolly Varden fry are omitted because few were caught. (A = channel edges, B = willow edges, C = debris pools.)

155 steelhead, and 13 sockeye in the upper river and 471 coho, 17 steelhead, and 14 sockeye in the lower river. In November, coho and steelhead fry also were more abundant at the upper than at the lower river sites (Table 1).

Parr Densities and Habitat Use

Coho, steelhead, and Dolly Varden parr densities (fish/100 m²) differed significantly ($P < 0.05$) among habitat types at both the upper and the lower river sites. Parr densities were consistently

greater in willow edges and debris pools than in channel edges (Figure 4). In the upper river, peak densities of coho (281, June), steelhead (82, August), and Dolly Varden (44, June) were in willow edges. In the lower river, peak densities of coho (36, July) and Dolly Varden (35, July) were in debris pools, whereas peak steelhead density (44, July) was in willow edges.

Within the same habitat types, mean density of coho and Dolly Varden parr was usually significantly ($P < 0.10$) greater at the upper than at the

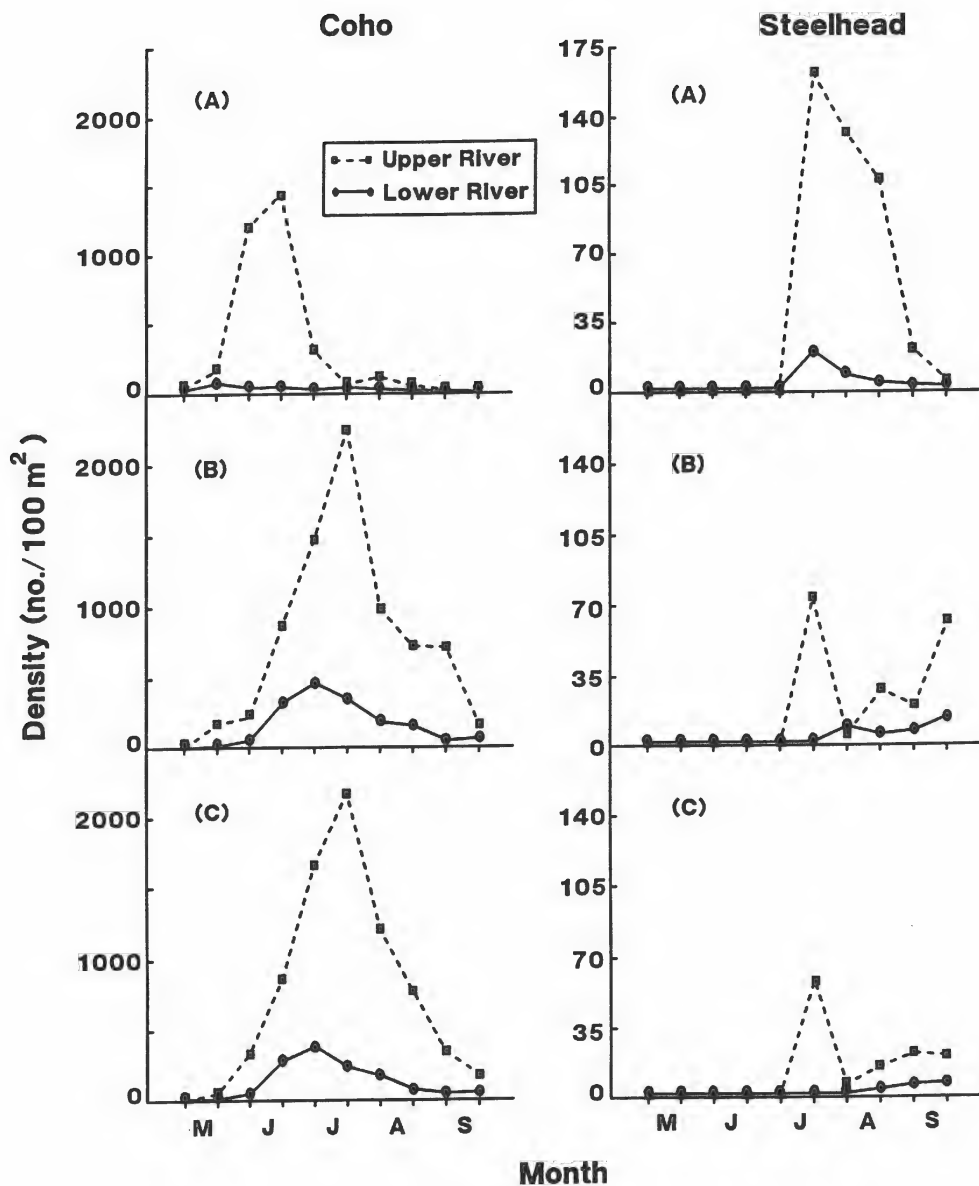


Figure 3. Mean density of coho salmon and steelhead fry (age 0) by habitat type in the upper and lower Situk River, Alaska. Sampling occurred biweekly from May through September 1989. (A = channel edges, B = willow edges, C = debris pools.)

lower river sites, whereas steelhead parr density was similar ($P > 0.10$) (Figure 4). Exceptions for coho and Dolly Varden were in channel edges and debris pools, respectively, where densities were

similar ($P > 0.10$) between the upper and lower river sites. In November, 97% of all parr caught were in the upper river, and 93% were Dolly Varden (Table 1).

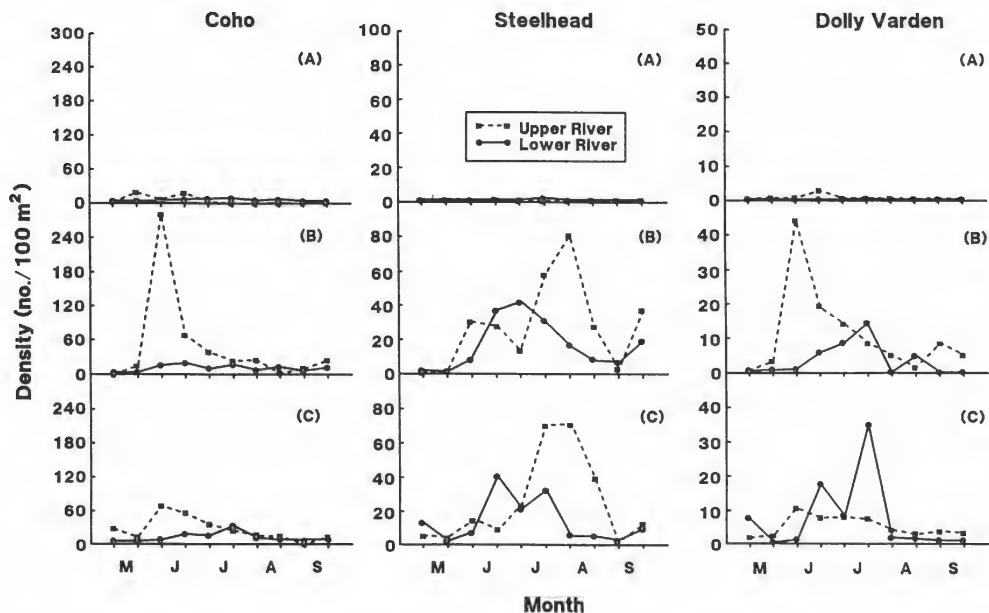


Figure 4. Mean density of coho salmon, steelhead, and Dolly Varden parr (age ≥ 1) by habitat type in the upper and lower Situk River, Alaska. Sampling occurred biweekly from May through September 1989. (A = channel edges, B = willow edges, C = debris pools.)

TABLE 1. Catch of juvenile salmonids in baited minnow traps set for 24 h at upper and lower Situk River sites on 30 November 1989. Two willow edges and two debris pools were sampled in each area of the river.

	Number of fry (age 0)		Number of parr (age ≥ 1)		
	Coho salmon	Steelhead	Coho salmon	Steelhead	Dolly Varden
Lower river					
Willow edges	78	123	0	1	1
Debris pools	63	54	0	0	0
Total	141	177	0	1	1
Upper river					
Willow edges	122	95	1	2	36
Debris pools	247	173	0	1	27
Total	369	268	1	3	63

Fish Length

Length of fry of all species generally increased from May to September, but was similar in late September and November. Monthly mean fork length of fry (all habitat types in lower and upper river combined) increased from 36 to 64 mm for coho (May–November), 32 to 43 mm for sockeye (May–July), and 32 to 61 mm for steelhead (July–November). Fry of all species (all habitat types and sampling

periods combined) were significantly ($P < 0.001$) larger at the lower than at the upper river sites (Table 2).

Length of parr of all species generally increased in most habitat types from May to August and declined thereafter. From May to August, monthly mean fork length (all habitat types in lower and upper river combined) increased from 60 to 86 mm for coho, 63 to 105 mm for steelhead, and

69 to 100 mm (May-July) for Dolly Varden. In September, monthly mean fork length was 83 mm for coho, 79 mm for steelhead, and 81 mm for Dolly Varden. Parr of all species (all habitat types and sampling periods combined) were significantly ($P < 0.001$) larger at the lower than at the upper river sites (Table 2).

TABLE 2. Fork length of juvenile coho and sockeye salmon, steelhead, and Dolly Varden (all sampling periods and habitat types combined) in the upper and lower Situk River, Alaska, May-November 1989. Data are means $\pm$ 1 standard error; sample sizes in parentheses.

Species	Stage	Fork length (mm)*	
		Upper river	Lower river
Coho salmon	fry	48.4 $\pm$ 0.2 (5195)	61.1 $\pm$ 0.2 (3178)
Coho salmon	parr	73.2 $\pm$ 0.4 (1065)	77.7 $\pm$ 0.4 (594)
Sockeye salmon	fry	33.0 $\pm$ 0.3 (123)	37.7 $\pm$ 0.7 (132)
Steelhead	fry	43.9 $\pm$ 0.3 (1262)	54.3 $\pm$ 0.9 (304)
Steelhead	parr	90.3 $\pm$ 0.7 (911)	98.3 $\pm$ 0.9 (677)
Dolly Varden	parr	75.6 $\pm$ 0.8 (386)	101.5 $\pm$ 1.6 (260)

*All fork lengths were significantly ($P \leq 0.001$, t-tests) larger in lower river than in upper river.

Discussion

Different habitat types in the main-stem Situk River provide important rearing habitat for different life-history stages of juvenile salmonids. Channel edges are important nursery areas for newly emerged fry, particularly coho in May, June, and July; sockeye in May and June; and steelhead in July and August. Coho, steelhead, and Dolly Varden parr primarily used willow edges and debris pools—areas with abundant cover. Results of trapping in late November suggest that coho and steelhead fry and Dolly Varden parr rear in willow edges and debris pools in late fall and probably in winter.

Few sockeye fry were caught in the Situk River after early July, and presumably most migrated to the estuary. Many sockeye fry in the main stem probably migrate to sea their first summer with-

out spending a winter in fresh water (ocean type). Two separate emigrations of sockeye fry exist in the Situk River: an early emigration of newly emerged fry into the estuary in March and April and a later emigration of larger sockeye to the estuary in May and June (Thedinga *et al.* 1993). Most ocean-type sockeye probably originate from Old Situk River; scale analysis shows that 94% of the sockeye escapement to Old Situk River (about 3,000 sockeye) have no freshwater annulus (Alaska Department of Fish and Game 1990). Numbers of ocean-type sockeye peak in the Situk estuary in May and June, and most fish leave the estuary and go to sea by late July (Heifetz *et al.* 1989).

The greater densities of most species and life-history stages in the upper than in the lower river could be due to differences in habitat or food resources. Warmer water and abundant seston in outflow from Situk Lake could contribute to more suitable habitat and a more productive forage base in the upper main stem, thereby promoting greater densities of some species such as coho and Dolly Varden. Steelhead parr density, however, was similar in the upper and lower portions of the river, indicating that habitat and food resources that possibly promote greater densities of coho and Dolly Varden parr were not as important for steelhead. Availability of seston in the lake outlet drift could also benefit some species more than others. For example, in the lower Taku River, Alaska, at a site influenced by lake outlet flow, stomach contents of juvenile sockeye contained an abundance of crustacean zooplankton from the lake, whereas chinook and coho stomachs contained relatively few (Brownlee 1991). In addition, most coho and steelhead spawning is in the upper watershed (Thedinga *et al.* 1993); as they emerge and disperse, more fry might occupy habitat close to the spawning areas in the upper river than farther downstream. This could explain, for example, why peak coho fry density was at least three times greater at the upper than at the lower river sites.

Seasonal differences in parr density between the upper and lower sites of the Situk River probably reflect immigrations from wintering areas and subsequent emigrations to the ocean. Coho and Dolly Varden parr were most abundant in the upper river from late May to late June as they left wintering areas (e.g., Situk Lake) and moved into the main stem. Substantial numbers of coho, steelhead, and Dolly Varden parr reared in the lower river from late May to late July, but numbers had

declined by early August, as some parr probably transformed to smolts and emigrated to sea. By late November any remaining parr had probably moved upstream to wintering areas. Some juvenile coho in Porcupine Creek, Alaska, emigrate upstream from the estuary to freshwater areas in fall (Murphy *et al.* 1984).

The larger size of juvenile salmonids in the lower than in the upper Situk River could be related to lower fish density. For most species, higher densities at the upper than at the lower river sites probably prevented faster growth. In laboratory studies with low- and high-density groups of coho and steelhead fry, the low-density group demonstrated greater growth (Fraser 1969). In addition, recruitment of emergent fry to upriver sites through summer probably resulted in lower mean sizes.

Potential Impacts of Flooding

Flooding from Russell Lake could severely impact the Situk River from its confluence with Old Situk River downstream to the estuary (Figure 1). Average discharge could increase from 6 m³/s to about 220 m³/s during flooding, and exceed 1,100 m³/s during peak flows (Mayo 1988). The main stem could widen from 25 m (average) up to 2,500 m, and the "new" river will be cooler and turbid from glacial influence and increased sediment loads. The old-growth forest on the floodplain will probably be flooded, causing debris torrents.

Rearing habitat and food production will probably be altered by flooding. Willow edges and debris pools could be scoured, filled in, or washed away. Initially, food production will probably be depressed. Invertebrate populations in a Wisconsin stream remained low for 1 year after severe flooding (Elwood and Waters 1969). Habitats will probably be unstable for several years as the river channel adjusts to increased flow and to changes in sediment and debris loads.

Eventually the Situk River will stabilize as it forms a new channel. New willow-edge and debris-pool habitats will form in time. Loss of some main-stem rearing habitat could be partially offset by expanded rearing habitat in secondary floodplain channels and sloughs (Clark and Paustian 1989). The future Situk River could resemble the glacial Taku River near Juneau, Alaska. Peak flow of the Taku River in summer (>700 m³/s; Murphy *et al.* 1989) is about the same as the predicted peak

flow of the future Situk River. Although the main channel of the Taku River is too swift (1 m/s) for juvenile salmon, its channel edges, sloughs, backwaters, and wetlands provide important rearing habitat for juvenile chinook, sockeye, and coho (Murphy *et al.* 1989). More rearing habitat could become available with the creation of Russell Lake. Flooding could also redistribute fish into nearby rivers (Figure 1).

The cooler, turbid floodwaters of Russell Lake could affect the distribution and growth of some fish species in the Situk River. Studies of the glacial Taku River show that sockeye rear successfully in turbid waters (<350 NTU), whereas coho and steelhead avoid the turbid river and rear in clearwater tributaries or off-channel beaver ponds (Thedinga *et al.* 1988, Murphy *et al.* 1989). Coho, however, rear successfully in the less turbid (<100 NTU) Kenai River, Alaska (Bendock and Bingham 1988). Fish growth will probably be slower after flooding because of lower temperatures, reduced forage, and increased turbidity. In the lower Taku River, coho fry average 50 mm FL in September (Murphy *et al.* 1989) compared to nearly 65 mm FL in the lower Situk River.

The ocean-type life-history strategy of sockeye in the Situk River could disappear after flooding. Because of cooler water and slower growth, ocean-type sockeye that now rear in the flood zone (main stem and Old Situk River) for 3-4 months could remain in fresh water for a year or more before smolting. Longer freshwater residence could result in increased mortality. Conversely, ocean-type sockeye could survive and even flourish after the river stabilizes. In the glacial Taku River, ocean-type sockeye rear successfully in side sloughs and beaver ponds (Thedinga *et al.* 1988).

Flooding of the Situk River will be a natural catastrophe that will affect habitat and the distribution and growth of some fish species for many years. However, with information from this study, fisheries managers can identify strategies to restore juvenile fish and habitat that may be lost from the flooding. Thedinga *et al.* (1993) predicts that 2.8 million juvenile coho, 586,000 Dolly Varden, 85,000 sockeye, and 62,000 steelhead could be lost due to flooding. Some potential restoration strategies in the Yakutat area may include off-channel development of groundwater spawning channels, rearing ponds, and egg-incubation facilities.

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Book Reviews

On the Home Front: The Cold War Legacy of the Hanford Nuclear Site

Michele Stenehjem Gerber. University of Nebraska Press, Lincoln. (Cloth, \$35.00)

On July 16, 1945 the world's first atomic bomb (and first man-made, uncontrolled chain reaction) took place at the Trinity test site in Alamogordo, New Mexico. The bomb's fissionable material was plutonium (^{239}Pu) produced at the Hanford nuclear production complex in the Columbia Basin of southeastern Washington state. The Hanford Engineer Works, code name for Hanford in those days, also produced the plutonium for the bomb that was dropped on Nagasaki on August 9, 1945, ending the war in the Pacific. Hanford had produced the bomb-grade plutonium in the remarkably short time of twenty-nine months. It was another incredible achievement that could be added to the growing list of successes enjoyed by the Manhattan Project, virtually the largest engineering project in the history of the world.

With the end of the "hot" war with Germany and Japan, however, came an even more protracted war with the Soviet Union and then mainland China: the cold war. Shortly after the end of WW II the Soviet Union demonstrated its nuclear capability leading to "deterrence" as the military strategy of the day. In the U.S. this meant the production and stockpiling of nuclear weapons, including plutonium bombs. For several years Hanford was the only plutonium producing facility in the United States, and it continued producing plutonium until 1987. So, the story of nuclear energy in the United States is, to no small degree, synonymous with the story of Hanford itself. Hanford was "there" from the beginning and stayed on for as long as it was needed. It could be justifiably proud of its overawing technological successes and of its role in safeguarding democracy. Indeed, for most of its history Hanford attracted enthusiastic support from not only the thousands of its employees, but also from politicians, community leaders, journalists, and citizens in the Tri-Cities area where the facility was located.

But years later came the revelation that Hanford had a dark side. In February 1985 the Department of Energy (DOE) released approximately nineteen thousand pages of previously clas-

sified documents of Hanford's early history, with fifty thousand more pages released over the next five years. Amidst all its technological achievements, amidst all the reverie in those achievements and amidst all the patriotic support of Hanford it was revealed that over the years radioactive and chemical wastes, far beyond tolerable limits, had been released to the air, ground, and water (Columbia River) surrounding Hanford. While accidental releases were themselves distressing, it was even more distressing to learn that some of the releases were deliberate, often part of scientific experiments. The very real possibility exists that Hanford seriously imperiled the health and safety of workers and proximate residents, as well as people many miles downwind and downstream of the facility. That dark side—its details still not fully known since available documents have not yet been fully analyzed and many more documents remain classified and unavailable—continues to shadow the facility today. What accounts for the dark side? What happened, and why? These unavoidable and compelling questions demand serious scholarly scrutiny. *On the Home Front: The Cold War Legacy of the Hanford Site* by Michele Stenehjem Gerber attempts, via a careful digging of archival documents, to do just that.

The author begins her account, appropriately enough, with a brief, but marvelously written background about the region; its geography and geology, its initial exploration, the Indians that were native to the region, and the eventual waves of settlers. These background features are then nicely woven into the account of how Hanford, a 640 square mile plot of desert, was chosen as the world's first plutonium production complex. The first consideration was remoteness: no town with a population greater than 100 persons was to be within 20 miles and no highway or railroad was to be within ten miles. Remoteness served the dual-purpose of safety and secrecy. There was worry that a chain reaction could get out of control leading to an explosion and it was generally known at the time that radioactivity could be dangerous, so with fewer people the extent of any exposures would be limited. It was clearly known that secrecy was a guiding principle of the entire Manhattan Project, so with fewer people there was less chance

that secrecy would be compromised. The other principal site considerations were technical, the need for vast quantities of water to cool reactor cores and the need for large quantities of electricity needed to power the facility. The Columbia River could provide both. So well-suited was the tract to the requirements of plutonium production that the decision selecting Hanford was made within a month of its initial site survey by military experts. It is a true irony of modern history that a decision that would significantly impact the area for many, unknown number of years into the future would be made in the astoundingly short time of one month.

The first reactors at Hanford were single-pass systems, drawing water from the Columbia River to prevent their overheating and then—after short term cooling—pumping the water back into the river. Through the cooling cycle the water collected radioactive materials and chemicals that it then deposited back into the river; over the years water containing radioactive and chemical wastes totaled billions of gallons. Once in full operation the facility, the author tells us, released 13,300 curies of radioactivity per day. Eight reactors of this type were built between 1944 and 1955, continuing in operation until 1964 when President Johnson began a scale down of uranium and plutonium production facilities. All were finally shut down by 1971.

Radioactivity was also released into the air regularly. Indeed, during the first two years of operation 420,000 curies of radioiodine ^{131}I (a threat to the thyroid, especially through the food chain) were released into the atmosphere. Added to these radioactive by-products of plutonium production was the deliberate release in December 1949 of nearly 8,000 curies of ^{131}I in an experiment known as the Green Run. The ground and soil, too, were the recipients of radioactive emissions. Upwards of 100 billion gallons of low-level, liquid radioactive wastes were disposed of via seepage into the ground and later via drilled wells. High-level wastes (principally long-lived alpha ray emitters) totaling 10 million cubic feet were stored in buried 149 single-shelled storage tanks, later augmented by double-shelled storage tanks. After twenty years the single-shelled tanks developed leaks; during the decade of 1962 to 1971 there were eight significant leaks with the most serious one releasing 50,000 curies of Cesium (^{137}Cs). All in all, in the course of its operations as the nation's largest

weapons production site Hanford generated the largest volume of nuclear waste in the Western world.

One unstated principle that is recurrently illustrated in the book is the principle from the science of ecology that says: "You cannot do only one thing." Over and over again actions by Hanford scientists, engineers, and technicians led to "other things," that is, unanticipated consequences, that required second-order solutions. Following the principle a step further the "solutions" themselves often led to other things. One of the more memorable of these resulted from the creation of huge waste-water cribs and various other stillwater ponds, pools and trenches at the facility. These became very favorable breeding grounds for mosquitoes, a problem heretofore unknown in the region, leading to a "mosquito plague" in the wider Hanford area. The solution?: a DDT aerial spraying program over the parks along the Columbia River, a program that continued even after the carcinogenic effects of DDT began appearing in the scientific journals.

Another recurring theme is even more disturbing. Over and over again production pressures and time demands relegated health and safety to secondary and tertiary importance. At the same time, workers and citizens were constantly reassured that radioactive emissions from the site posed no health hazards. The credibility of these claims had to be taken at face value because their scientific basis rested upon government research, not peer-reviewed science, and because the operations at Hanford were shrouded in the tightest possible secrecy. So, even if those exposed wished to independently verify government claims there was literally no way to do so. It was eventually learned that many of the government's assurances were unfounded. For example, infants living in the Hanford area during the war years who drank milk from backyard cows received some of highest doses of radiation ever imposed on a group in America. Even people as far away as Spokane, to the northeast, received excessive doses of radioactivity.

Overall this is a book of great but failed promise. It becomes preoccupied with chronicling the changing production practices at Hanford, the studies conducted by Hanford health scientists to determine tolerable doses of radiation, and the actual levels of radioactive release to the air, land, and water of the Columbia Basin. The reader is presented with a vertiginous collection of facts

(replete with a dizzying number of official acronyms), but rarely do we find reflection on, let alone synthesis of, what the facts mean for the larger issues raised by the book. In addition, the book is poorly organized; the useful photographs are not integrated into the text, there is an absence of appropriate transitions between topics, and the chapter on advances in radiology (Chapter 7) should appear before the chapters on releases so that readers can gauge the seriousness of the releases. Added to these problems is a maddening editorial disregard for the general, educated reader. The most vexing example of this is the gross neglect to inform the reader of the various types of radiation (alpha, beta, gamma, X-rays) and of the relationship between the half-dozen measures of radiation (curies, rads, roentgens, particles per square foot, micrograms, microcuries per kilogram, etc.) used in the book, as well as what they mean.

This book contains all the raw material for a tale of high drama and intrigue and, more importantly, for a lesson on how to balance national security, secrecy, and technological priorities of the state against the rights of citizens to health and

safety, and the right to be informed when those enjoyments are threatened. But it fails these tasks. Tucked in among the vast stream of historical facts Gerber raises, almost as an afterthought, the most pivotal question of the Hanford legacy: "Does the public need to wait until all the technical questions have been answered conclusively, or is there not a way to have reasonable, ongoing public discussions of potential risks and uncertainties during the period in which newly emerging technologies mature?" (p. 75). It is a question that is neither confined to Hanford, nor to any of the other facilities in the vast complex of nuclear technology, but rather it is one of the most important political questions about technology of our era. Unfortunately, *On The Home Front* wends around it, choosing instead to emphasize the historical details of Hanford, rather than its larger historical and political meaning. This was the largest of the book's unrealized goals and, for me, its greatest disappointment.

—Eugene A. Rosa
Department of Sociology
Washington State University
Pullman, WA 99164-4020

Ecological Integrity and the Management of Ecosystems

Edited by Stephen Woodley, James Kay, and George Francis. St. Lucie Press, Delray Beach, Florida, 1993. (Cloth, \$59.95)

As the 20th century draws to a close, human society is undertaking a self-appraisal of its track record on environmental stewardship on an unprecedented scale. The reasons for this are complex. Psychologically, they may stem from an innate sense of good or, conversely, from a sense of guilt. They may even reflect an evolutionary trend in a species that once stood erect to survey its new world and is once again standing erect to see what a mess it has made.

Ecological Integrity and the Management of Ecosystems is about the concepts, frameworks, and measures being considered to monitor the health of Canada's ecosystems. The message is urgent as recent legislation, such as the 1988 amendment to the Canadian National Parks Act, has given reality to the phrase "ecosystem integrity." No longer can the concept hide in implicit human values; we now need explicit statements to fall back on because we have made ourselves accountable by law.

The book comprises eleven articles divided into two main sections, "Setting the Stage" and "Applying the Concepts." While the division appears logical, the actual boundary is fuzzy as most authors have dealt with both conceptual and applied issues. The closing article by Kay should be in its own section ("Synthesis"?); it is helpful to read first for its thumbnail sketch of the main ideas covered although Kay expresses his own bias for a thermodynamics based approach. The book is attractively bound in a glossy shades-of-green hard cover. The articles are non-technical and, generally, reader-friendly. In the brief Preface the two core questions are asked that tie it all together: "Does ecological science have the ability to provide useful measures of ecological integrity?" and "Is there a useful process for incorporating value judgements within measurable ecological variables?"

Regier sets the stage with an abstract discourse on what ecosystem integrity is. Some parts are bewildering such as the figure depicting ecosystems being shaped by intrinsic organizational pressures (forces of good?) and human cultural influences (forces of evil?). Other parts are more informative. For example, I was intrigued by the classification of human attitudes toward nature as exploitist, utilist, integrist, and inherentist. After laying the blame for

our environmental woes at the feet of capitalist/socialist bureaucracies, Regier concludes that the current ecological tool box offers only limited hope for a way out. He advocates a "comparative empiricism" approach combining holistic perception with analytical understanding. Regier ends by taking the reader on a mystical journey through a space-time dimension in which all the properties of an ecosystem with integrity are laid bare.

King follows with a plea for the importance of scale and hierarchy in ecosystem monitoring and management. An ecosystem perspective, he argues, should be applied at all scales of observation as this would help tie together results from individual studies. Structural and functional understandings of ecosystems are needed, but some structures such as rare species may be expendable with little impairment to function. Greater attention to natural "integrators" of function, for example discharge points in watersheds, tree rings, and top level consumers would help to ensure consistency in monitoring efforts. Aside from an irksome statement that fine scale measurements will lead to cause-effect understanding, King offers an otherwise clear overview of hierarchy theory and its practical potential.

Third on stage are Steedman and Haider, reminding us that socio-economic voices must also be listened to in formulating notions of ecological integrity. They outline the strategic choice model (SCM) as a potentially useful tool to integrate opinions of various interest groups. This was developed in the field of market research to determine why tourists choose certain holiday destinations and appears to involve a multivariate analysis of human choices. The presentation is, however, brief, and the example to illustrate the method using a northern Ontario lake left me unconvinced.

Keddy et al. close the first section drawing on their extensive experience to propose a pragmatic approach to the integrity assessment of wetlands. Similar to King they suggest that monitoring be confined to a few "state" variables, including biotic indicators such as diversity and total plant and amphibian biomass, and abiotic indicators such as water and nutrient levels. Keddy's vision for a Wetland Integrity Guidebook offers a worthwhile goal to focus attention on these biologically valuable and threatened Canadian ecosystems.

Karr leads off the applied section calling for a multidisciplinary approach in aquatic ecosystem management. Clean water is not enough he argues. Needed are good reference systems to set standards

for habitat quality, organic inputs, flow regimes, and biotic interactions. Karr's index of biological integrity (IBI) appears promising, but the brief example does not, in my opinion, do it justice. There is a strong underlying message here and in other articles throughout the book calling for more education in systematics and ecology; ironically, these very subjects are currently facing severe funding threats in Canadian universities.

In his article, Munn reveals a definite spatiotemporal bias for what an ecosystem is: "the appropriate time horizon for assessing ecosystem integrity is half a century". He offers several practical guidelines for monitoring, including the use of UNESCO world heritage site selection criteria, and various socio-economic indicators such as sales of cars, toilets, and air conditioners. Although helpful, these practical suggestions were, at times, mixed into a more conceptual background requiring some effort to disentangle one from the other.

Marshall et al. outline the Canadian government stand on the issue through the newly formed State of Environment (SOE) Reporting, the responsible body set up under Canada's Green Plan legislation. As expected, the emphasis is on coordinating activities, developing partnerships, identifying (and, hopefully, filling) data gaps, and reporting information. This is a truly laudable venture into an enormous task; the first steps have been taken at a workshop organized for the Atlantic Region held in Halifax in 1991.

Shackell et al. continue with the theme set in the preceding article. Following a broad sweep over the national landscape, they briefly present the main findings of the Halifax workshop. A case is made for the establishment of "intensive" and "extensive" monitoring stations within each of 15 "ecozones" into which Canada has been carved. Although the plan is to record change rather than status quo conditions, it remains to be seen whether there is a strong enough political will to make the long term funding commitments that this plan requires. The three classes of integrity indicators proposed by SOE—"stressors," "exposures," "responses"—are described, and a rather baffling flowchart is given to show how the administrative process will work. Also included is a table showing actual workshop results in matrix form. While this gives a useful synopsis, my ecological intuition led me to think that there should be more "D's (deficient information), particularly in the stressor column labeled "Natural Disturbance." The overall tone is optimistic and encouraging despite recognized deficiencies in base-

line inventories and functional understandings for most ecosystems.

Woodley's article deals with implementing procedures following the 1988 amendments to the laws governing national parks. These are the flagships of Canada's conservation enterprise and, as Woodley points out, require both general and threat-specific monitoring. He outlines nine measures, each with a strong biological focus. Synthesis and communication of information to user groups presents special challenges, and the "amoeba" diagram that Woodley borrows from a group of Dutch researchers appears to be well suited for this purpose.

In contrast to the general tone of other articles in this book, Reynoldson and Zarull present a specific problem analysis of contaminated sediments and impacts on benthic invertebrates in the Detroit River. As a group, bottom sediments in aquatic systems are probably facing the most serious threats because they accumulate toxins and because they are, for the most part, hidden from view. The case is strongly made for monitoring chemical and biological factors, particularly benthic invertebrates which are the organisms most directly affected. Although I found the application of numerical procedures interesting, the strong emphasis on comparing mathematical methods may leave the general reader wondering about the overall relevance to integrity. I was reminded of Regier's earlier concern that analytical fire-power will not, on its own, provide us with all the answers that we are seeking.

All in all, *Ecological Integrity and the Management of Ecosystems* is a timely ideas book in the aftermath of recent political decisions to monitor and sustain the integrity of Canada's ecosystems. On its success in answering the two core questions posed in the Preface, I give it an A— on the first (availability of measurement tools) but only a C— on the second (integration of scientific and public perceptions). Reaching a workable consensus over what an ecosystem is, let alone whether it can be monitored for integrity, represents a formidable challenge. One hopes that the analogy of the human patient who is being regularly monitored for a series of low-level infections and dies any way because of the cumulative weakening effects, will not apply to Canada's ecosystems.

—Gary E. Bradfield
Botany Department
The University of British Columbia
Vancouver, B.C. Canada V6T 1Z4

Defining Sustainable Forestry

Edited by Gregory H. Aplet, Nels Johnson, Jeffrey T. Olson, and V. Alaric Sample. Island Press, Washington, D.C., 1993. (Cloth, \$49.95, ISBN 1-55963-233-X; Paper, \$24.95, ISBN 1-55963-234-8)

Semantic skirmishing over resources management jargon is a continuing theme of the field. Currently, myriad actors in the "sustainable forestry" game are debating the definition of sustainable forests and forestry, as others have argued in the past about carrying capacity, sustained yield, and other shibboleths of resource credibility. Fortunately, *Defining Sustainable Forestry* has emerged early in the current debate to help us understand the various philosophies and approaches represented. While the book cover claims the contributors come "closer to reaching consensus on the definition of 'sustainable forestry,'" there is no attempt within to forge a consensus. The rather provocative set of visions about our current forest dilemmas better serve the reader than whatever bland consensus could have been forged. *Defining Sustainable Forestry* is an essential volume for those interested in the future of forestry.

The book is presented in three segments: Part I focuses on the objectives of sustainable forestry; Part II contains regional approaches to sustainable ecological systems; and Part III introduces social and policy considerations in defining sustainable forestry. Each section is introduced by one or more of the editors, and they do an admirable job of summary and interpretation of the 3-6 chapters in each section. The difficulty in assigning chapters to a section mirrors the difficulty of defining sustainable forestry: is this social, or biological, or both? Some chapters (e.g., Honadle's Institutional Constraints chapter in Part I and Romm's chapter in Part III on sustainable forestry as an adaptive social process) could have easily fit into other sections as the one to which they were assigned.

I found the first and third parts of the book the most interesting and having the longest "shelf life." Part I begins with a provocative first chapter by Reed Noss, who defines sustainable forestry as a smoke screen "behind which we chip away at our biotic heritage," and as "sustainable exploitation." In Noss' view, the issue can be narrowly defined as a biocentrically-oriented "sustainable forest" issue, which is considered independently of the so-

cial and political arenas of compromise in which "forestry" occurs. A Forest Service trio provides the closest response in this segment of the book. Hal Salwasser, Douglas MacCleery, and Thomas Snellgrove provide a very broad, and therefore somewhat unfocused, view of "new directions" in Forest Service management. They allude to "new forestry" and "new perspectives" while validating past emphases on sustained yield and multiple use, validating some of Noss' prejudices. Much of the chapter deals with historical demand for resource outputs, implying a continued focus on output-related management that helped generate the current forest dilemmas. The latter part of the chapter effectively summarizes their view of sustainable forestry as the intersection of ecological, social, and economic spheres.

Part II presents a series of regional treatments of sustainable forestry. The sharpest treatment is provided by Jerry Franklin for the Pacific Northwest, in part because this area has been the crucible for change in land management philosophies. Franklin does his usual concise and persuasive job, although it is a bit dated (the conference was in 1992 so no mention is made of Forest Ecosystem Management Assessment Team process [FEMAT, or President Clinton's "Forest Plan"] which occurred in 1993, and is in litigation in 1994). The bookend chapter of this section, by John Gordon, is a short, pithy summary of ecosystem management as a process to attain sustainability, rather than a goal in and of itself. Both Gordon and Franklin have been on the "cutting edge" of forest planning in the last several years, and this has undoubtedly sharpened their perspectives. The intervening chapters are less engaging, and seem to show most other regions of the United States are still groping for the nature of the problems as much as for solutions. Chapters on the Northern Hardwood Region, Central Hardwood Region, Southeast, and Inland Northwest seem to downplay the role of institutions in sustainable solutions to forest issues, although they summarize well some of the ongoing research approaches to biodiversity protection.

Part III provides a social and political context for sustainable forestry. I thought this to be the most invigorating section of the book. Alice Rivlin notes that the social and political system of North America is designed to resist change. Jeff Romm's chapter on sustainable forestry as an adaptive social process is a strong counterpoint to Reed Noss'

introductory chapter. Romm calls sustainability a political word that denotes conflict, and symbolizes both resistance to change that people do not want and demand for change that people do want. The sustainable forest is an issue precisely because it cannot be defined. The reader is left wishing that Noss and Romm could have had a more direct exchange of ideas.

The editors present a brief conclusion, and by so doing let the chapter authors carry the primary load. They conclude with a hope that the ideas presented will catalyze continued explorations of

the meaning of sustainable forestry. I think their hope is realized. With our plethora of interacting natural and cultural systems, we should expect the "right" answers to change over space and time. Readers should not expect one clear definition, but will be stimulated to think about the complexities of the multiple meanings of sustainable forests and forestry.

—James K. Agee
College of Forest Resources (AR-10)
University of Washington
Seattle, Washington 98195

The Biology and Management of Red Alder

Edited by David E. Hibbs, Dean S. DeBell and Robert F. Tarrant. Oregon State University Press, Corvallis, 1993. (Cloth, \$22.95)

Red alder is among some 35 species in the genus *Alnus*, and species in 24 other diverse genera that are hosts to the nodule-forming, soil actinomycete *Frankia*. *Frankia* fixes nitrogen from the air symbiotically in alder root nodules, allowing alder to grow on soils lacking available mineral nitrogen. Organic nitrogen from red alder tissue accrues in the soil primarily through the deposition of deciduous leaves and other litter and through turnover of root tissue. The resulting increase in soil nitrogen fertility can benefit other plants growing together with or succeeding alder, particularly on raw soils.

Red alder is the most common hardwood tree species in the Pacific Northwest. It is a pioneer species intolerant of forest understory conditions. Red alder has rapid juvenile growth and is relatively short-lived. It tolerates poor soil drainage and seasonal flooding, but is intolerant of droughty conditions. The best stands occur on deep alluvial soils where it is found in greatest abundance, though it also occurs widely on upland sites.

These characteristics afford great opportunities for managing red alder for multiple benefits to people, but until recently red alder was regarded by most forest managers as an aggressive weed to be eradicated because it competed with Douglas fir regeneration following clear cutting. There has long been a small group of scientists, including Dr. Robert Tarrant and other contributors to the book, as well as some forest managers and an industrial group founded in 1955 called the Western Hardwood Association, who extolled the virtues of red alder. However, only recently have market conditions made red alder commercially competitive with conifers, resulting in significant industrial, political, and scientific support for this tree species in Oregon and Washington. Unfortunately the legacy of several decades of alder "weed control" programs is a scarcity of young alder trees. This scarcity is a cause of concern to the growing alder industry of the Pacific Northwest.

Red alder's new found economic importance, together with the rapid advances that are now being made in our understanding of the biology,

management, and utilization of this tree species, make this book particularly timely. Interest in managing and using red alder is at an all-time high. In the case of red alder there is an existing base of biological information available in advance of widespread management of the species, which the book's authors and editors have appropriately noted is a rare instance in the history of forestry. Research efforts devoted to red alder were often viewed with skepticism or met with ridicule in the past. The small group of red alder researchers in universities, public agencies, and private industry has been vindicated. Their research is paying off.

This book is a synthesis of current knowledge of the biology and management of red alder. It is divided into two sections, the first section devoted to the biology of alder and the second to its management. Thirty four authors have contributed to create seventeen chapters that combine reviews of previously-published information with results of current research.

The first section on the biology of alder covers diverse topics of a basic nature. Chapters in this section are devoted to actinorhizal (*Frankia*) and mycorrhizal symbioses, genetics, nitrogen fixation rates and controls, influences on soils and long-term productivity, water relations and photosynthesis, growth patterns, stand development and succession, ecological characteristics, and wildlife interactions of red alder. It is apparent from these chapters that physiological and genetic research on red alder and its symbionts lags behind ecological research. The chapters give a good overview of the current state of knowledge concerning red alder. In many cases, gaps in knowledge concerning red alder are dealt with by reference to research on other similar tree species. Surprisingly little research has been done on the interactions of red alder with wildlife or on the role of alder in hydrological and ecological processes of streams and rivers.

The second section builds on the first in presenting current principles and practices of red alder management. Chapter topics include site quality evaluation, seed technology, nursery practices, plantation establishment, stand management, fertilization and nutrition, growth and yield, wood quality and economic potential for red alder. As wild stands of red alder become less available for harvest, there will likely be increases in red alder plantation establishment on appropriate sites. The development of cultural methods for growing red

Alder in plantations is still in its infancy, but much progress has been made as described in this book. The current technology and potentials for improving establishment of red alder seedlings via *Frankia* inoculation are discussed, but the importance of this technology is yet to be established.

The book maintains its focus on red alder in the Pacific Northwest with an emphasis in the second section on management for timber. In so doing it does not become unwieldy. Forerunners of this book have focused more broadly on the biology of all alders or have combined the topics of red alder wood utilization and the economics of management with biology and management, with less success at being comprehensive and coherent. As interest in red alder and other alder species continues to grow, there will be a need to compare alder management systems throughout the world and to assess the potential of red alder as an exotic plantation species, but that will require a different forum.

This book will be of particular interest to forest managers in the Pacific Northwest, biologists interested in alders and other nitrogen fixing tree species, as well as those managing alder or other temperate hardwood tree plantations elsewhere. The book is published with an attractive hard cover. It contains photographs and figures in black and white, which undoubtedly help to keep the price of the book low. Photographic reproductions are only fair in quality. The book, being a collection of symposium papers, is often repetitious as each set of authors sets the stage for individual chapters or puts their own spin on a particular topic. But these are minor distractions that do not detract greatly from this book's success in synthesizing current technical knowledge of the biology and management of red alder.

—Jeffrey O. Dawson
Department of Forestry
University of Illinois at Urbana-Champaign
Urbana, Illinois 61801

Principles of Conservation Biology

Gary K. Meffe, C. Ronald Carroll, and Contributors.
Sinauer Associates, Inc., Sunderland, MA, 1994.
600 pages (Cloth, \$46.95)

The interdisciplinary field of conservation biology has existed over a decade without a textbook. Not only has there been no adequate reference covering subjects ranging from genetic diversity to economics to the "tragedy of the commons," but teaching in this area has been difficult. Anyone who has taught a conservation biology class, with an eye toward real-world applications without skimping on rigor or theoretical foundations, knows the frenzy of compiling reading lists from dozens of journals and chapters of assorted edited books.

To fill this void, *Principles of Conservation Biology* bursts onto the scene in a profoundly important and useful way. It is well written and impressively edited—with a near total lack of the irksome typos often accompanying first editions—and the glossary and index are extensive and thorough. Although ideas will inevitably change in a field as rapidly evolving and fast-moving as conservation biology, the book is also remarkably up to date, with careful attention to recent literature and a considerable number of 1993 and even 1994 citations. As might be expected in a book integrating field studies, case histories, and political conflict, issues in the Pacific Northwest of the U.S. are well-featured.

The book is presented in four sections. The first, "Introductory Concepts," introduces the biodiversity-related problems facing the world and the operational conundrums facing the field of conservation biology. To this end, different chapters address values and ethics, pattern and process of biodiversity loss, and biological and legal definitions related to "species" as the currency of biodiversity discussion. In the first chapter, Meffe and Carroll set an impressive tone that is followed throughout the book: rigorous in thinking, broad in understanding, while also enthusiastic and hopeful in outlook. Here they also establish the fundamental theme that conservation biology is dynamic, not static, and make a useful distinction between a modern "nonequilibrium" view and the "equilibrium" view held by Aldo Leopold and other major players in the history of the conservation field. The authors continue to grapple with complexity and conflict, and to avoid banal platitudes, when they present their list of 3 guiding principles

that "should permeate all aspects of conservation efforts": a) evolutionary change; b) dynamic ecology; c) human presence.

The second of the four major sections is "Population-Level Concerns," which gives a solid introduction to the interplay between genetic and demographic processes in population dynamics at the local and landscape scale. At this point it becomes clear (and the authors emphasize) that this text assumes a knowledge of genetics, population genetics, and population ecology, and that it cannot substitute for a background in ecology and evolutionary biology. Inevitably, the need to cover rather sophisticated and complex ground with a minimum of review creates some rough spots. For example, the discussion of inbreeding and gene flow is a bit muddled and would have been clarified by discussion of Wright's F-statistics for subdivided populations, but such a topic was deemed to be beyond the scope of the book; instructors will need to supplement such areas. (Additional examples in later chapters include the dynamics of Allee effects and the ecological issues related to the Intermediate Disturbance hypothesis). Nevertheless, this section drives home an honest appraisal of "cookbook prescriptions" and "rules of thumb," going far toward encouraging students to grapple with the complexity of issues and decisions instead of just falling back on comfortable but often misleading quantitative guides such as the much-abused "50-500 rule" for Minimum Viable Populations.

Following the Population-Level concerns of the second section, the third section addresses "System-Level Concerns." Key subjects addressed in these three well-connected chapters include interactions between species that are lost from or added to a community, the difficulty of defining a "natural" community composition, and issues related to habitat fragmentation and the design of conservation reserves. Interestingly, the historically significant issue of SLOSS (Single Large or Several Small) is downplayed in favor of a view that the debate on optimum reserve size has moved beyond that, to a point where the most critical questions focus on "how to convince the human populace that large reserves are needed, and how to manage internal dynamics of and external threats to reserves once acquired."

The fourth and final section ("Practical Applications and Human Concerns") is the longest, consisting of eight chapters. This section focuses on

case studies and applications of previous chapters, as well as covering new ground on important topics such as ecological restoration, invasive species, policy-making, and economics. The much-debated terminology of sustainable yield and sustainable development are treated in a particularly careful, yet provocative, way. The book ends with a call to action; no punches are pulled, and the last few pages bring the reader back to the same issue that the book opens with: human population growth, and the inevitable impacts of 260,000 additional people on earth every day.

Half of the 18 chapters in the book are written by Meffe and Carroll, while the remaining chapters, and essays within the chapters, are written by dozens of contributors. Although having multiple contributors adds an impressive level of primary expertise on the plethora of sub-specialties in the field, it probably contributes to my only real complaint about the book: it is sometimes inefficient in coverage, and therefore repetitive, on certain topics. For example, subjects such as metapopulations and genetic drift are scattered throughout many chapters, patched together with a number of "As will be seen" or "As previously discussed" transitions, which can be frustrating in a book this large. Even worse, there are inconsistencies between authors of different chapters; although debate and individual thinking should be at the heart of conservation biology (as Meffe and Carroll state convincingly in the first chapter), without synthesis or moderation the opposing views can be simply confusing or misleading.

The three to five essays within each chapter add considerably to the length of the text, but they are well-integrated into the flow of the chapters and often add illuminating perspectives from experts

in particular sub-disciplines. Some of my favorites were those by S. A. Temple on "The role of the University," S. J. O'Brien on "The U.S. Hybrid Policy," and E. P. Pister on "The importance of value systems in management." An instructor choosing to use this book as the primary text in an upper-level or graduate course may be forced by time constraints to eliminate some of the essays from required reading, but most of the essays will be appreciated for their in-depth perspectives.

In sum, the book does an outstanding job of addressing both the ecological/conceptual basis of conservation biology and the real-world problems faced by managers and policymakers, making it a vital text for both students (upper level or graduate) and practitioners of conservation. And the authors put their money where their mouth is, stating that 1/3 of the royalties from the text will be donated by the authors and publisher to two major conservation organizations, "in hopes of turning student book costs into actual conservation gains."

Perhaps the most exciting characteristic of this book is that it imparts knowledge and wisdom while remaining humble and openminded, an approach summarized in the opening of Chapter 16: "We challenge students and professional scientists alike to question all present conservation practices and policies (including those presented throughout this book)." To think, to learn, and to act to benefit conservation. Valuable lessons from a conservation biology text that succeeds in its mission.

—L. Scott Mills
Dept. of Fisheries and Wildlife
University of Idaho
Moscow, ID 83844-1136

Saving Nature's Legacy: Protecting and Restoring Biodiversity

Reed F. Noss and Allen Y. Cooperrider
1994. Island Press, Washington, D.C.
(Cloth, \$48.00; ISBN 1-55963-247-X;
Paper, \$27.50; ISBN 1-55963-248-8)

By all appearances, preservation of natural resources is among the top issues of public concern in the United States in the last decade of the 20th century. Reports of environmental problems, dwindling natural resources, and conflicts among those who use natural resources appear daily in local newspapers and on television and radio. Major issues that repeatedly surface include loss of natural resources from urban growth, protection of threatened or endangered taxa and anadromous fish stocks, dwindling supplies of both second and old-growth forest resources, a general reduction of anadromous fish runs, toxicity of pollutants such as dioxins, and a reduction of the ozone layer. It is no wonder that the late 1980s and early 1990s have seen a renewed proliferation of books dealing with environmental issues and conservation.

The stated purpose of *Saving Nature's Legacy* is to present an exercise in "applied conservation biology." Its primary goals are to convince readers that biodiversity is worthy of preservation and to provide land managers and interested individuals with guidelines for conserving biodiversity. The authors wrote the book because they believed that most efforts to preserve biodiversity were inadequate. They recognize, and freely acknowledge, that what they propose will require decades to implement and depends on stabilizing (if not reducing) human population and reducing consumption of natural resources. To achieve their objectives, the writers reviewed a considerable body of literature (much of it unpublished) and freely interspersed their philosophy throughout the book. The book contains good material but it is sometimes difficult to differentiate between the authors' opinions and results of peer-reviewed scientific research.

The first two chapters introduce the concept of biodiversity, describe values of biodiversity, and discuss how biodiversity is created and affected by various land management practices. Refreshingly, the authors include genetic, species, community or ecosystem, and landscape or regional diversity in their definition. The authors also note that biodiversity occurs at a broad range of scales, and, there-

fore, conservation efforts must also consider the same range of scales.

The introductory material is followed by three chapters on nature reserves, their history (very brief), selection, and design. The authors point out that protecting the "hotspots" of biodiversity and endemism and "representative" communities is inadequate to protect total biodiversity. Gap Analysis and Nature Conservancy and natural heritage program databases are discussed as a first step in the selection of reserves. Other criteria suggested for consideration include population dynamics, dispersal, and the scale of natural disturbances (e.g. fire). The authors recommend that a network of interconnected reserves with differing degrees of protection (i.e. zoning) be considered as a solution—an estimated 25-75% of a particular landscape or region would require fairly stringent protection to preserve all native biodiversity.

Management of forests, rangelands, and aquatic resources is treated in separate chapters. Each chapter begins with a general discussion of ecological principles and is followed by a description of how management practices have negatively affected biodiversity. The authors then review alternative approaches to management in varying detail and present their suggestions for the methods they perceive will best conserve biodiversity. Many of the recommendations, such as protection of riparian areas from grazing and logging, are not new ideas and make sense. Others such as the elimination of clearcutting and logging by non-mechanical means (i.e. with horses) are also not new and will be difficult to implement. The reader may be disappointed that more new ideas are not presented. Even so, the authors do attempt to synthesize a considerable body of literature in these chapters and have provided some thoughtful solutions to rather sticky problems.

The final two chapters of the book deal with monitoring and the future. The monitoring chapter mainly points out that the results of management efforts must be checked—else their success or failure will not be known. The concepts presented here are good, but it is written as if land managers have not considered monitoring results of their activities. This may be true in some cases, but in many others, monitoring has not been accomplished because monetary resources were unavailable rather than for a lack of consideration. Monitoring also requires continuity of funding—not something government agencies are prone to

receive. The book concludes with a summary that gives the reader some suggestions on how to accomplish the ambitious goals the authors have set forth and a reminder to spend some time outdoors.

This book certainly achieves some of the objectives set forth by the authors. It provides guidelines for land managers and individuals interested in preserving biodiversity and directly states many of the authors' ideas and opinions without apology. However, reading the book is sometimes arduous. Each chapter contains direct criticisms of current (and often past) land management techniques; individuals who disagree may stop reading and miss

many of the good ideas presented here. This does not mean the criticisms are unjustified, but some of the methods that are criticized have already changed, or are in the process of changing. This book is definitely worth reading—whether or not it becomes a “bible for wildlands managers,” as suggested by a review comment on the book jacket, remains to be seen.

—Edward G. Schreiner
National Biological Survey
Olympic Field Station
600 East Park Avenue
Port Angeles, Washington 98362

Northwest Science

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1994

Volume 68, Special Issue

SPECIAL ISSUE

NORTHWEST SCIENCE



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David L. Peterson
Cooperative Park Studies Unit
College of Forest Resources
University of Washington, AR-10
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Editor's Note

Many landscapes of the Pacific Northwest have been dramatically altered by human impacts without adequate consideration of long-term biological and social impacts. There is currently a growing awareness that we need a broader landscape perspective to address natural resource issues because of the many linkages within and between ecosystems. There is also increased interest in the restoration of functions and processes that have been affected by past land use practices. In this special issue, the authors take a detailed look at how river basins of eastern Oregon and Washington have been modified over the past two centuries. The connection between deterioration of fish habitat and the utilization of other resources is clearly stated. The articles in this issue are intended not as a gloomy portrayal of the past. Rather, they document fundamental changes in riverine systems and provide a scientific basis for future resource management activities. Policies with greater emphasis on the protection of fish habitat can be viewed as a potential source of conflict or as an opportunity for change. In any case, decisions about natural resources in the next few years will have impacts for generations to come.

Communication regarding scientific issues should be directed to the senior author of each article. Additional copies of the special issue can be obtained by contacting either of the senior authors.

—The Editor

Northwest Science Special Issue 1994

Environmental History of River Basins in Eastern Oregon and Washington

Preface

As I write (April 1994), the season's fish count data indicate that this year's spring chinook run in the Columbia River Basin will be the lowest in about 30 years. The same data indicate that next year's spring chinook run will be even lower. Throughout the Pacific Northwest, salmon fishing has been either eliminated or sharply curtailed.

Many factors have contributed to the collapse of the Columbia River Basin's salmon and steelhead, but the available information clearly indicates that hydroelectric development and the pandemic degradation of tributary spawning and rearing habitat are the primary causes for the continuing loss of this once great natural resource. The degradation of aquatic habitat is the connecting thread, not only in the precipitous decline of salmon populations, but also resident fish such as bull trout in the John Day River basin and Northern Rockies, Lahontan cutthroat in the Great Basin, and cutthroat in the Northern Rockies.

The two papers of this Special Issue present the grisly details of the history of land-use in some of the larger salmon-bearing watersheds of the Columbia River system. Some of this information has been available to those who were willing to dig prodigiously through large multi-volume reports, scattered graduate theses, or non-peer reviewed "grey literature." For the first time, the papers in this special edition present the information comprehensively in a peer-reviewed format with a relatively wide distribution.

The geographic context is important because most research on land-use and fish habitat interactions has occurred west of the Cascade Mountains, as is also the case with attendant adjustments in resource policy. Meanwhile, salmon populations in the interior have been extirpated (in the case of many coho populations), listed under the Endangered Species Act (ESA), Snake River chinook salmon), or petitioned for listing under the ESA (bull trout).

The geographic context also has its legal context; federal mandates for water quality and resource management must be met everywhere. The Columbia River Treaty Tribes reserved the right under the treaties to take fish destined to pass through their "usual and accustomed" fishing places. These include the fish produced in the interior Columbia basin. The courts have affirmed that this right is more than the right to dip nets into empty waters. The federal government must ensure that its activities are consistent with producing fish for the taking for the Columbia Basin Tribes.

There is also a socioeconomic context. All communities dependent on fish are suffering. Although much has been made of the havoc wreaked on timber-dependent communities by curtailing logging, many communities are undergoing severe economic duress due to the lack of salmon, part of which is attributed to the aquatic consequences of recent logging. Balance needs to be restored. Clearly, we cannot have both high levels of commodity extraction and healthy watersheds with robust fish populations.

In the scientific context, both papers illustrate the importance of historic baseline data. Over the past several years, the research community has generally not favored the collection of baseline data unless some sort of hypotheses could be tested with it in the short term. The work of McIntosh *et al.* (this volume) indicates that, perhaps, we need to reverse current thinking: unless we collect baseline data we will not be able to make inferences in the short or long term.

For years, available research on streams has indicated that pool losses occur as sediment loads are increased or woody debris is lost. Any sagacious analyst could have concluded that land management activities had probably led to pool loss, but there remained the question of how much

pool habitat had been lost over recent decades. Without specific documentation of the magnitude of pool loss, such analysts would have probably been termed "Cassandras." The work of McIntosh *et al.* provides regional answers to that question. We now know that in some systems pool losses have been tremendous because of land-use activities. Although pools may not be the best indicator of stream health, the pool data clearly indicate that the rivers of the interior Columbia basin have been severely damaged. The work of Wissmar *et al.* (this volume) provides the historical context on how watershed degradation has occurred over the course of less than two centuries. Given the information in these two papers, it appears, in the clarity of hindsight, that the "Cassandras" in the aquatic resources professions may have been optimists.

The data are, indeed, alarming. As go the waters of the planet, so go we. As Paul Ehrlich and Edmund Wilson have stated, "If there is to be any chance of abating the loss of biodiversity, action must be taken immediately . . . The indispensable strategy for saving our fellow living creatures and ourselves in the long run is, as the evidence compellingly shows, to reduce the scale of human activities . . . Unless humanity can move determinedly in that direction, all of the efforts now going into in situ conservation will eventually lead to

nowhere, and our descendents future will be at a risk."

A number of approaches have been suggested as a means to arrest and reverse the damage done to watersheds, and they run the gamut from letting scientists fix it to more citizen participation. But regardless of the route chosen, nature has a distinct bottom line. Talk, alone, will not restore ecological functions. It is easier for us to change than to change natural laws. If we do not change, all water-needing creatures, from salamanders to ourselves, will suffer more over time.

Now that the numbers have been quantified, the biggest question is when will practices be adjusted? When will resource specialists and policy makers begin to use the best available information to avert problems like the ones documented in these papers before they occur? When will natural resource managers be able to become something other than coroners?

The people who depend upon fish for their way of life are waiting for the answers to these questions. The fish are waiting, too, though fewer by the moment.

Jonathan J. Rhodes
Columbia River Inter-Tribal Fish Commission
729 NE Oregon St., Suite 200
Portland, OR 97232

A History of Resource Use and Disturbance in Riverine Basins of Eastern Oregon and Washington (Early 1800s-1990s)

Abstract

A historical review of human activities influencing stream and riparian ecosystems in eastern Washington and Oregon shows that cumulative effects of resource uses and management over the past two centuries are altering the health of many river basins. Past practices such as livestock grazing and forest harvest near riparian areas and streams became collectively significant over long time periods and are continuing today. Case histories for the Okanogan and Methow River basins (north central Washington), the Naches River (eastern Cascade Mountains), and the Grande Ronde and John Day River basins (eastern and north central Oregon) provide chronologies of events that shaped the present-day landscapes and socio-economic conditions of the region. Historic cumulative effects on stream and riparian ecosystems include livestock grazing and mining from the 1860s until about 1910. Timber harvest, roads, fire management, dams, irrigation, and fisheries increased in importance during the 20th century. Management histories show minimal actions for reducing damage to stream and riparian ecosystems. Managers commonly perpetuate the notion that streams and riparian areas are difficult to manage because little is known about how these ecosystems function. Many agencies strive to develop procedures for treating the symptoms of degraded ecosystems while giving little consideration to the causes. Other agencies and public groups concerned with conflicting issues like water allocations and minimum instream flows for fish usually disagree with plans for resolving these issues. The continuous dissent by these parties only adds to the plight of fish as available water and habitats continue to decline. Alternatively, new basin-wide management strategies of federal and environmental organizations offer hope for improving the ecosystem biodiversity and population levels of fish and wildlife. Priorities include the protection, restoration, and monitoring of habitats and networks that connect stream and riparian ecosystems in degraded and intact watersheds. Intact watersheds (e.g., roadless and wilderness areas) function as critical habitats and refuge areas for fish and wildlife of adjoining ecosystems.

Introduction

As a result of President Clinton's Forest Summit in Portland Oregon during Spring 1993, considerable attention is being focused on the influences of forest and other resource management practices on the health of Pacific Northwest ecosystems. Management recommendations of an inter-agency team of scientists point to the urgent need for improvements in ecosystem management (Forest Ecosystem Management Assessment Team 1993). Some management plans call for the conservation and restoration of fish species and stocks that could be listed as threatened or endangered species on federal lands. Of particular concern to the Forest Service in the Pacific Northwest is the restoration of salmon stocks, habitats, streams, and riparian ecosystems of upland forests. A primary objective is to return ecosystem functions and connectivity

towards "natural conditions" that meet the historical requirements of fish and wildlife. Some major questions that need to be answered are, "How have historical ecosystems functioned and how have human actions changed them?"

This document reviews the environmental history of the influences of human activities in eastern Oregon and Washington over the past two centuries. The purpose is to (1) document the chronology of events of resource uses and management practices that cumulatively shaped present-day landscapes of stream and riparian ecosystems and (2) provide baseline information for referencing and evaluating past and future management actions. Case histories of select river basins provide representative chronologies for riverine landscapes throughout eastern Washington and Oregon (Figure 1). The histories document the effects on the environment caused by individual and cumulative impacts of livestock grazing, management of forests, water storage and allocation, agriculture, road construction, flood control, and mining. Additional historic documentation about factors causing losses of salmon stocks and habitats in eastern Washington and Oregon can be found in McIntosh *et al.* (1994a,b).

¹School of Fisheries (WH-10), University of Washington, Seattle, Washington 98195

²Department of Forest Science, Oregon State University, Corvallis, Oregon 97331

³USFWS Oregon Cooperative Fishery Unit, Oregon State University, Department of Fish and Wildlife, Oregon State University, Corvallis, Oregon 97331

⁴Pacific Northwest Research Station, USDA Forest Service, 3200 SW Jefferson Way, Corvallis, Oregon 97331

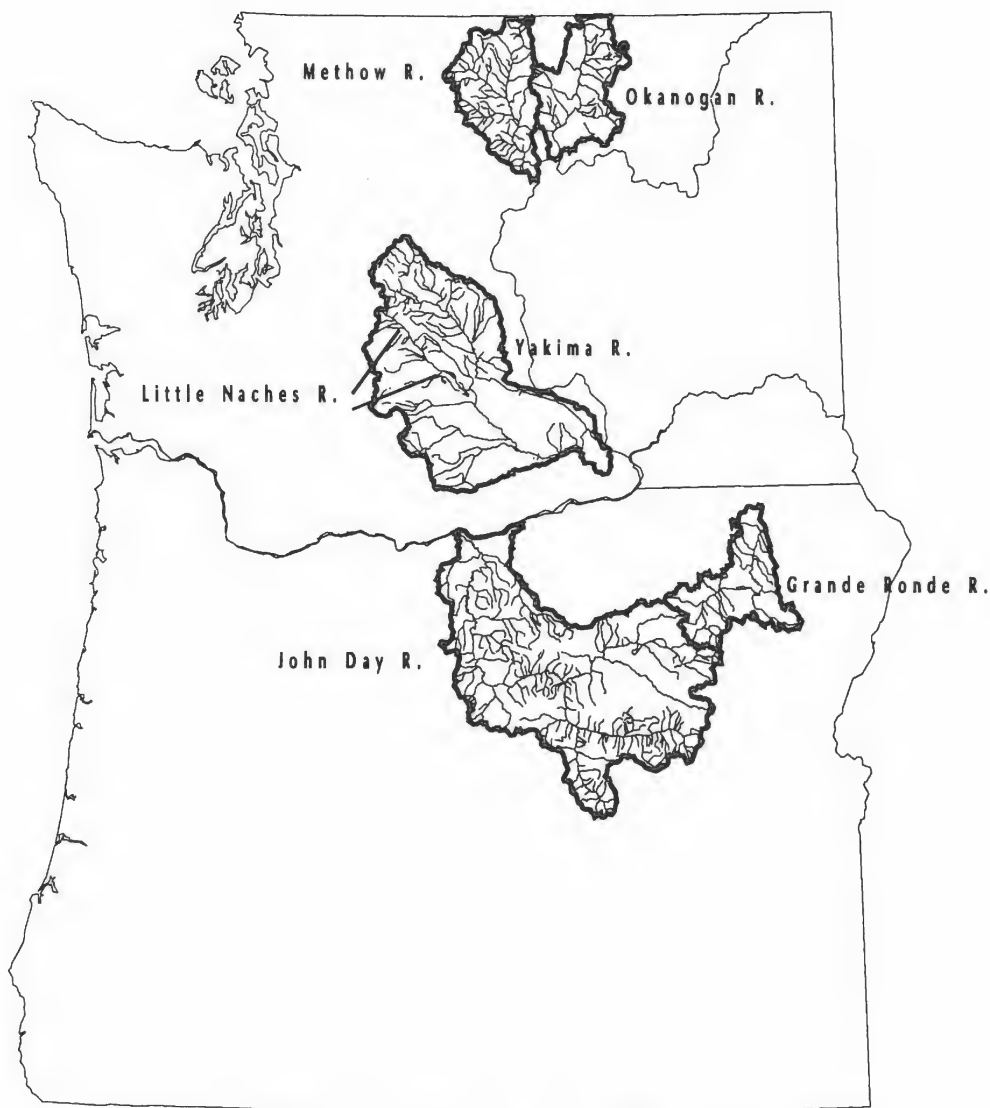


Figure 1. Map of the major tributary rivers of the Columbia River drainage in eastern Washington and Oregon. The locations of river basins of the case history studies are noted in bold type.

The management history focuses on practices designed to address problems and issues of the different resource uses. Important examples include the cumulative effects of livestock grazing, logging, and roads on soils and waters and on issues involving water allocations and instream flow

requirements for salmon. We conclude by reviewing recommendations for new basin-wide management strategies that include ecosystem perspectives and emphasize long-term protection, restoration, and monitoring activities.

Historic Resource Uses in Select River Basins

The case histories include four river basins, the Okanogan and Methow (north central Washington), the Little Naches River of the Yakima River drainage in the eastern Cascade Mountains, the Upper Grande Ronde River basin (Blue Mountains of eastern Oregon), and the John Day River basin in north central Oregon (Figure 1). The Okanogan drainage area includes the Similkameen River basin and covers about 21,238 km², with 6,475 km² within the boundaries of the United States (Figure 1). The Methow River valley lies just west of the Okanogan River and has a drainage area of 4,662 km². The Little Naches River, a fifth-order basin (398 km²) in the central Cascade Mountains, lies in the headwaters of the Naches River, a tributary of the Yakima River drainage. The Upper Grande Ronde River basin (3,000 km²) originates in the Blue Mountains of eastern Oregon and drains into the Snake River. The John Day River in the high desert of north central Oregon has the fourth largest drainage area in the state (21,072 km²). Important sources of historical information that describe settlement patterns and related developments in eastern Washington and Oregon include Steele (1904), Kerr (1931), Dicken and Dicken (1979), Highsmith and Kimerling (1979), Holstine (1987), Wilson (1990), Portman (1993), and Wissmar *et al.* (1994).

Okanogan and Methow River Basins (North Central Washington)

The historical chronology of settlement, natural resource uses, and conflicts of the Okanogan country represents a mesocosm or time capsule of the events and developments that shaped the present-day landscapes and socio-economic conditions in eastern Washington and Oregon. The Okanogan valley (Figure 1), as well as most of north central Washington, was isolated but not insulated from the principal east-west corridors of commerce in the Pacific Northwest. The location and the late arrival of the railroad slowed development and preserved frontier-like conditions into the 20th century. Fur trading, overland exploration, mining, encounters between Euro-Americans and Native Americans, creation and modification of Native American reservations, cattle drives, homesteading, conflicts between sheepmen and cattlemen, overgrazing of ranges, railroad building, irrigation

development, logging, and dam building were all significant aspects of frontier life and the development of north central Washington. Many of these activities had substantial impacts on land and water resources. The major activities influencing streams and riparian areas can be seen by following a chronology of early historical events (Table 1). Most of the early settlement history activity occurred in the Okanogan valley, with homesteads not appearing in the Methow River Basin until the 1890s. Portman (1993) provides an excellent history of the Methow valley, describing settlement patterns and related social and economic developments during the twentieth century.

Early Settlement, 1810-1860s

The British first established a presence in the region with the beginning of the fur trade in 1811. In 1816 the British-owned North West Co. built Fort Okanogan at the same site as J.J. Astor's trading post. Furs from British Columbia (New Caledonia) and Fort Colville were collected and shipped downstream, and supplies were received from Fort Vancouver at the mouth of the Columbia. In 1821 Hudson Bay Co. took over the North West Co. During 1834-36 the original Fort Okanogan was replaced with a new Fort Okanogan closer to the Columbia River.

The large influx of immigrants to Oregon during the 1840s ensured American control of Northwest, with the result that in 1846 the international boundary was set at the 49th parallel, ending joint occupation of the Oregon territory by British and Americans. The following year the Hudson Bay Co. discontinued fur trade between British Columbia and Fort Okanogan, effectively ending British and American fur trade in the general area. Between 1858-1861 most of the British presence in the area involved surveying the 49th parallel.

The next decade was relatively quiet until 1858, when a gold rush to the upper Fraser River resulted in movement of large parties of miners on the Cariboo Trail along the Columbia and Okanogan rivers. The previous discovery of gold in the vicinity of Colville and the Yakima River of Washington in 1855 had already incited miners to emigrate to the north country (Steele 1904). In 1859 gold was discovered in the lower Similkameen River valley near the Enloe Dam west of Oroville, Washington (Table 1). The booming population of 1,200-3,000 miners conducted

TABLE 1. Chronology of major settlement, natural resources, and related developmental events in north central Washington. Asterisks (*) indicate historical activities having potential impacts on riparian and stream habitats of headwater tributary streams and river valleys. Major sources of information include Steele 1904, Kerr 1931, Wilson 1990, and Portman 1993.

Date	Event	Activity
1811	Fur trade begins	John Jacob Astor (Pacific Fur Co.) establishes trading post at the confluence of the Okanogan and Columbia Rivers
1816	Fur trading	*Supply of beaver nearly exhausted in the Okanogan country suggesting beaver removal changed riparian and stream conditions.
1846	U.S.-British boundary	International boundary set at 49th parallel.
1847	Fur trade ends	Hudson Bay Co. ends fur trade
1853	Washington Territory created	Isaac Stevens first governor of Washington Territory
1855	Yakima Reservation created	Yakima Indian Reservation created (1.2 million acres)
1858	Gold discovered in British Columbia	*Gold rush on the Cariboo Trail in the Okanogan country
1859	Gold discovered in Okanogan	*Gold discovered in lower Similkameen. Placer mining of river channel and banks may have degraded the river ecosystem.
1860-1880	Water diversion in lower Methow River	*China Ditch constructed above mouth of Methow River to deliver large volumes of water to sluice boxes for placer mining suggest potential damage to riparian and stream habitats. Facility converted to irrigation in the 1920s by the China Ditch reclamation district, destroyed by 1948 flood.
1860s	Cattle drives on the Cariboo Trail	*Overgrazing of ranges suggests potential for erosion in the floodplains of the Okanogan River. cattle drives on the Cariboo Trail supplied mining towns in B.C.
	Settlement in Okanogan	Hiram F. Smith near Lake Osoyoss first resident cattle rancher.
	Salmon harvest	*Weir across the Okanogan River by whites and catching salmon leads to possible over-harvest of returning adult fish, about 20 wagon loads of salmon per day.
1870	Population, 34 non-Native Americans	Federal census of the Okanogan valley.
1872	Colville Reservation created	Colville Indian Reservation formed to resolve land ownership questions caused by patterns of white settlements. Area east of Okanogan River included today's Ferry County (2.5 million acres).
	1872 Mining Act	First regulation of mining claims.
1878	Population, 44 non-Native Americans in Okanogan	Stevens County census. Area of Stevens County from 1864 until 1888 included today's counties of Okanogan, Chelan, Ferry, Stevens and Pend Oreille.
1879-1880	Moses reservation created	Area west of Okanogan to crest of Cascade Mts. and from Lake Chelan north to the 49th parallel.
1880s	Settlements increase in Okanogan valley	*Population of settlers begins to increase suggesting land clearing and conversion of riparian areas.
1886	Okanogan mining boom	*Mining boom began west of Okanogan River and miners, ranchers and settlers move onto the Moses Reservation. Placer mining of river channel and banks, lode mining and numerous poorly designed concentrating and flotation mills, high daily water demands (e.g., 60,000 gallons), and production of sediment wastes may have impacted river ecosystems.
	Moses Reservation	Moses reservation opened to miners and settlers.
1883-1916	Railroads	See Text
1888	Okanogan County created	Included today's Okanogan & Chelan Counties.
1889	Washington becomes a state	
1890	Population of 1,509 non-Native Americans in Okanogan	Okanogan County census. Okanogan County included today's counties of Okanogan and Chelan.

continued, next page

TABLE 1, continued

Date	Event	Activity
1893	Okanogan mining declines	Price of silver declines during U.S. recession.
1894	Flood	*100 year flood and debris-dam break flood destroy towns of Conconully and Silver. High probability of major changes in stream and riparian habitats.
1890s	Mining in the Methow	Slate Creek District (Mammoth Mine) near Hart's Pass supplied by new town of Winthrop (1891). The Red Shirt & Alder Mines of the Twisp district were major producers.
1895	Mining resumes in Loomis District	*Numerous rich mines resume operations. Ten years of intense lode mining (1895-1905) and numerous poorly designed concentrating and flotation mills, high daily water demands, and production of sediment wastes may have degraded river ecosystems.
1897	Washington Forest Reserve	Washington Forest Reserve established by President Cleveland.
1899	Okanogan County reduced in size	Formation of today's Okanogan & Chelan Counties. Populations were 2,839 in Okanogan and 1,321 in Chelan counties (Steele 1904).
~1900	Sheep arrive in Okanogan	*Sheepmen begin to settle in the Okanogan.
	Sheep drives	*Overgrazing of summer ranges suggest increased erosion of watersheds and modification of riparian & stream habitats.
1905	Irrigation development	*Removal of water from rivers and streams reduced or negated the development of riparian & stream habitats.
~1910	USFS created	
+1915	Mining in the Slate Creek District	*The Azurite Mine near Hart's Pass and the Ballards (1918-1934) and ASRGO (1934-1942) periods. Road construction along the upper Methow River and tributaries.
+1916	Railroad and highway construction	*Alteration of river valleys leads to erosion, removal and constraint of riparian and stream habitats.
1916	Homestead Act	*Opened homesteading and decreased open range.
+1920	Logging	*Alteration of watersheds leads to erosion, changes in hydrologic and geomorphic features of riparian and stream habitats.
+1930	Dam building	*Created migration barriers for fish and alter river and riparian habitats for fish. Major changes include altered river flows, water temperatures, habitat carry capacities for fish and predator conditions.

intensive placer mining in the Similkameen River channel until they stampeded north to large gold strikes in the Fraser River and Cariboo areas of British Columbia during 1860. These strikes caused many miners to pass through the Okanogan country and resulted in the first settlement near Lake Osoyoos, Oroville, Washington. Mining claims in the United States were not regulated until the 1872 Mining Act.

In the early 1860s, settlers had a direct effect on salmon resources when they may have overharvested salmon runs in the Okanogan River. John Utz, who settled near Lake Osoyoos, constructed a weir across the river. He trapped as many as 20 wagonloads of salmon a day to sell to Native Americans. In combination with later impacts of intensive commercial fishing, the building of the

Columbia River dams, and habitat losses due to irrigation and other developmental projects throughout the Okanogan basin, these early actions devastated anadromous fish runs. Spring chinook salmon (*Oncorhynchus tshawytscha* [Walbaum]), native (endemic) summer/fall chinook salmon and steelhead (*O. mykiss* [Walbaum]) stocks were virtually eliminated, and sockeye salmon (*O. nerka* [Walbaum]) runs were depressed (Jim Spotts, Okanogan National Forest, pers. comm.).

Mining, Livestock, and Agriculture, 1860s-1910

From the 1860s to 1900 mining took place throughout the Okanogan country from the Chelan mountains eastward across the Methow to the Conconully Range. Although no documentation

exists of the direct effects of mining on stream and riparian resources, the possibility for impacts is implied by the extent and duration of mining activities. Some of the most extensive silver and gold strikes (placer and lode mining) were on Silver Creek in the Salmon and Ruby districts northeast of today's Okanogan City, on Loop Loop Creek, and along the Similkameen River near Loomis. During the 1886-93 boom years, the Ruby-Conconully districts were considered among the richest mining areas in the Pacific Northwest (Wilson 1990). Other important districts were Palmer Mountain, Chesaw, Methow, and Twisp. Mineral production during the mining boom in Okanogan County ranked only behind Ferry, Stevens, and Chelan counties (Okanogan County was created in 1888 [Table 1]). The first discovery of silver and gold in the Methow valley was in 1887 at the town of Silver near Twisp. During the boom the abundance of other natural resources and the area's mild climate also induced increased settlement by farmers, stockman, and lumberman.

Maps of mining districts (Hodges 1897) suggest that numerous mining claims were located in and adjacent to rivers and their tributaries. Placer mining of river channels and banks, lode mining, and wastes from numerous poorly designed concentrating and flotation mills may have degraded several river ecosystems (35 to 40 mills in Okanogan County). A prime example of an affected system was Salmon Creek near Okanogan City. Salmon Creek was essentially destroyed by the rapid construction of the Ruby and Conconully town sites and development of claims throughout the drainage. By 1888 about 13 miles northeast of Okanogan City, Ruby City extended a quarter of mile within and adjacent to the channel of Salmon Creek. The destruction of Salmon Creek has been particularly devastating to spring chinook salmon (Jim Spotts, Okanogan National Forest, pers. comm.).

Mines of the region were supplied by stern-wheeled riverboats on the Columbia River from Wenatchee to Brewster and by the North Pacific Railroad. Railroads did not arrive in the Okanogan valley until 1916. Railroads came to Spokane Falls and Ellensburg in 1883, Colville in 1890, Wenatchee in 1892 (Steele 1904, Kerr 1931). The impact of railroads on population growth was very evident in Chelan County, where the population increased from 1,321 in 1899 (Table 1) to

3,931 in 1900, and 7,547 in 1903. Twenty percent of the county's population was in Wenatchee during 1903 (Steele 1904).

Cattle began to appear in considerable numbers during the 1860s in north central Washington (Table 1). The cattle were driven along the Cariboo Trail, which led to the gold strikes in the Fraser River and Cariboo mining districts. Extending 960 km (600 mi) from The Dalles on the lower Columbia River to the upper Fraser River valley, the Cariboo Trail supplied beef (mostly from the Willamette and Yakima valleys) to the northern mining camps via the Okanogan River valley. During the peak years of the cattle drives (1862-64), British customs at Osoyoos Lake collected duty on 7,720 cattle, 5,378 horses, 1,317 sheep, and 948 mules. Ben Snipes, a principal cattlemen using the Cariboo Trail, was reported at one time as having over 100,000 head of cattle and 20,000 horses grazing in the Yakima valley (Wilson 1990).

The Yakima valley was also the principal supplier of cattle for Seattle. The Seattle market was originally supplied with beef driven from the Yakima valley across Snoqualmie Pass. When the range of the Yakima valley became over crowded with cattle in the 1870s, the cattle company Phelps & Wadleigh shifted some of their operations to the Okanogan area. Phelps & Wadleigh was the largest cattle buyer in the Washington territory until the winter weather of 1880-81 forced them into receivership. Such weather demonstrated the problems of livestock grazing in the Okanogan valley throughout the year. Nevertheless, the cattle industry of the valley managed to survive. In 1896 cattle were being driven from the Okanogan valley to Wenatchee for shipment via the Great Northern Railroad to Seattle.

The Cariboo Trail opened the Okanogan country to the outside world and led to the first white settlers in the area in the early 1860s. Hiram F. Smith, the first resident cattle rancher of the Okanogan, settled near Lake Osoyoos around 1860 (Table 1). He also planted an apple orchard, ran a trading post, and made the first discovery of gold. The opening of the Colville Reservation in 1896 and boundary changes in 1898 led to changes in mining claims and premature staking of lands for farmland and stock ranges.

As settlers began to move into Okanogan County, the number of horses and other livestock climbed steadily between 1890 and 1905. Although these increases were considerable, other

counties with earlier settlement and growing populations as well as higher agricultural production, such as wheat, showed even greater increases in livestock. For example, in 1904 Whitman County had 26,706 horses and 44,074 cattle compared with Okanogan's 7,000 horses and mules and 21,058 cattle.

About 1900, sheepman began to settle in Okanogan County (Table 1), with the number of sheep increasing dramatically from <2,000 before 1890 to ~31,757 in 1904. Many other pre-settled counties had even more sheep. In 1904 Yakima, the greatest sheep-producing county, had about 147,000 sheep. Throughout eastern Washington and Oregon, sheep grazing attracted the attention of established cattle ranchers, who believed that sheep ruined pasture for livestock. One incident, near the town of Okanogan (during the winter of 1902-03), of sheep grazing in cow pastures resulted in a night raiding party and the slaughter of an estimated 900 sheep.

During the mid-1890s agriculture replaced mining as the principal economic activity. In Okanogan County between 1900 and 1903, crops increased from about 1,500 acres to 13,000 acres. Most farmable lands were located in converted river floodplains and wetlands. The extent of the Okanogan River floodplains and the presence of historic wetlands (mainly from Tonasket to Osoyoos Lake) were suggested by reports in 1882 of dense swarms of mosquitoes (Pierce 1882). By 1900 water was clearly limiting and irrigation projects were needed to sustain population growth and agricultural development.

The Okanogan Reclamation Project, authorized by Congress in 1905, was one of the first irrigation projects undertaken by the US Reclamation Service (Table 1). This project was approved without sufficient investigation into water supply in terms of the local climate and hydrologic regime of the watersheds. The Reclamation Service encountered problems not only because of the failure of the watershed to furnish sufficient runoff, but because of poor management practices. These problems included inexperienced contractors, water being put on lands with sandy soils not suited for irrigation, and public funds being misused by providing water for private lands. By 1931 when a majority of the irrigated land was under the Okanogan Irrigation District, electric pumps, not irrigation ditches, provided most of the water from the Okanogan River (Kerr 1931).

Irrigation systems undoubtedly caused major problems for migrating salmon. The main irrigation canals on the floodplains of Okanogan River, for example, were constructed parallel to the river channel, intercepting most tributary streams. Anadromous fish migrating from the main river appeared effectively blocked from entering tributary streams by these canals. Such irrigation canal systems appeared less extensive in the Methow and Similkameen River valleys.

The Little Naches and Naches River Basins (Central Washington)

This case history begins with an overview of early settlement (1850-1930s) and resource uses in the Naches and Yakima River basins and concludes with historic studies of habitats changes in the Little Naches River. Retrospective analyses of the Little Naches River describe long-term changes in stream and riparian habitats between 1935 and 1992 after the intense impacts of livestock grazing (pre-1930) and during periods of increased timber harvest. The Little Naches River, located slightly north and east of Mount Rainier, is a tributary of the Naches River in the headwaters of the Yakima River drainage (Figure 1). The Naches River basin provides summer and fall rearing habitat for 30% to 37% of the anadromous salmonid fry and smolts in the Yakima Basin (Fast *et al.* 1991). The basin also contains 59% of the remaining harvestable timber in the Yakima River drainage (Wenatchee National Forest 1990). In 1990, federal harvest plans targeted the Little Naches River as the primary area for harvest over the next decade (Wenatchee National Forest 1990).

Early Settlement, Livestock Grazing, and Agricultural Uses, 1850-1930s

Before 1850 the Naches and Yakima River basins were primarily unsettled by pioneers, and most of the population was comprised of Native Americans. Although the Native society was one of hunting and gathering, early irrigation canals for crop cultivation were built during the 1850s under Catholic missionary authority (Davidson 1953). Catholic missions at Parker Bottom, Tampico, and Nanaim were the first non-native settlements in the Yakima valley. Once the missionaries were established, the settlers followed rapidly.

The flow of immigrants was stimulated by the McClellan exploration party's survey of the Naches

Pass area for a route to Puget Sound during the 1840s (Gossett 1979). The first permanent settlers arrived around 1860 near Moxee, bringing several hundred head of cattle. Soon after, the Yakima Valley became one of the primary areas for cattle ranching east of the Cascades. Cattle were also driven into the headwaters of tributary river basins to graze in alluvial floodplains and glacial valleys. The cattle drives peaked in the 1880s.

Sheep grazing soon became one of the primary uses of the upper tributary basins. Sheep were driven along "driveways" into the upland forests for summer foraging. Sheep ranching peaked at the turn of the century and again during World War I when the demand for and value of sheep products were at their greatest. Records for 1907 indicate 260,000 sheep were permitted into the Naches and Tieton river basins (Uebelacker 1980). During this period, the Naches basin held 55% of the sheep grazing in the Yakima and 83% of the cattle and horses (S. Carter, Supervisor's Office, Wenatchee National Forest, Wenatchee, WA, unpubl. data).

By 1900 the public recognized that areas of the Forest Reserves were being overgrazed. Livestock grazing, the use of driveways, and burning of forests to promote pasture were in direct conflict with other uses of the forest like recreation, timber harvest and water for irrigation. Sheep and cattle driveways were established along most of the ridge crests between tributaries. Many of the ridges and tributary valleys contain naturally erosive soils and sparse vegetation that were impacted by sheep and cattle drives during summers and subsequent soil erosion in wet seasons. Between the 1850s and 1930s, soil erosion on hillslopes and valleys and inputs to streams were likely enhanced by several factors, including overgrazing by livestock, repeated burning practices to increase grazing areas, and wildfires (Smith 1993). Reviews of soil losses in upland areas that experience excessive grazing pressures suggest considerable erosion (Dunne and Leopold 1978, Sidle *et al.* 1985, Platts 1991, Swanston 1991).

A grazing allotment system was begun by the Federal government in the 1880s in response to complaints about the grazing and burning of the forests. The formation in 1897 of the Washington Forest Reserve, covering most of today's Okanogan, Wenatchee, and Mt. Baker-Snoqualmie national forests, facilitated the implementation of the allotment system. By 1909 the Menastash and Cle

Elum ridges and the main Taneum valley (areas east and north of the Naches River basin) were all closed owing to their overgrazed conditions. The loss of land and water resources and the closure of grazing areas caused large-scale conflicts between livestock ranchers and the burgeoning agriculture industry. In 1923 only six allotments were present in the Little Naches drainage (S. Carter, Supervisor's Office, Wenatchee National Forest, Wenatchee, WA, unpubl. data). Reports to Congress in the 1930s indicate that the grazing areas within the forest were heavily degraded (Anonymous 1930, Cooperative Western Range Association 1938). By 1930 the number of sheep permitted on remaining allotments was <10% of the historical peak numbers. By 1950 many allotments were either abandoned or severely reduced in number.

While the impacts of the sheep and cattle industry in the early days were heavily concentrated in tributary headwaters, burgeoning irrigation and agricultural developments were changing the Yakima River and tributary landscapes, as well as the economy of the area. In 1860 the Toppenish-Simcoe canal system was built near the Yakima Indian Reservation. By 1869 a large canal draining the Naches valley was irrigating lands below the confluence of the Naches and Yakima Rivers. Railroads and the construction of the Sunnyside Canal in 1893 further stimulated agricultural development. Irrigation and the extension of the Northern Pacific Railroad into the Yakima valley opened up thousands of acres of unarable land to development. Land used to grow hay and feed crops for cattle and sheep eventually gave way to row crops, permanent crops such as hops, grapes, and orchards.

Water Diversions and Fish, 1905-1990s

The Reclamation Enabling Act of 1905 empowered the Federal Bureau of Reclamation to appropriate waters for irrigation purposes, including eminent domain for rights of way for canals and reservoirs. No minimum fish flows or other fish protection measures were designated in the act. Between 1905 and 1915 the damage to migrating and resident fish populations was devastating. Many of these early systems, such as the Sunnyside Canal and the Tieton Canal, were constructed without fish ladders or screens, which were not required until the Fish Ladder Law was enacted in

1915. Although some fish ladders were built after 1915, screens that prevent juvenile salmon entrapment in the canals were not placed until the 1930s. Fast *et al.* (1991) estimate 90% of the annual runs of salmon and steelhead trout was destroyed by the early 1990s. Primary factors leading to the decline in salmon runs included construction of dams and canals without adequate fish passage facilities such as ladders and screens, log drives in river channels that eroded spawning and rearing habitats, and indiscriminate local and commercial fishing. These factors, together with increased water temperatures and low streamflows due to water diversions, and high suspended sediment loads and chemical pollutants from forest and agricultural runoff, comprise long-term cumulative effects (> 100 years) that have contributed to poor salmon survival.

The Little Naches River Basin, 1800s-1930

Historically, land uses in the Little Naches River basin included intensive livestock grazing (1880 to 1930), some selective timber harvest in floodplains, and recreation. The ridge crests along with riparian areas were heavily used as grazing, sorting, and driveway areas prior to the allotment system. Overgrazing and natural- and man-induced fires most likely damaged vegetation and soils, which led to erosion and the opening of riparian canopies of streams. Around 1850 a large and extremely hot wildfire burned most of the northwestern portion of the basin and two-thirds of the mainstem valley (Plummer 1902, Gossett 1979, Uebelacker 1980). This natural event, coupled with various land-use practices suggests long-term cumulative impacts across the riverine landscape. In the Little Naches River, chronically eroded areas have been identified in aerial photos taken ~50 years after burning and grazing activities (Smith 1993).

Historic patterns of recreational uses in the Little Naches River basin follow the road and trail systems and their continued expansion and improvement. As trails and roads improved, recreation became a year-round pursuit in the basin. In the late 1800s camping and picnicking along the alluvial flats were the first major recreational usages. As early as 1853 the Naches Pass Trail was the major wagon train route to the Greenwater River basin on the west side of the Cascade Mountains. In the early 1900s, prior to construction of the Chinook Pass (Highway 410), it was slated to

become a highway across the Cascades. Today, much of the trail includes Forest Service Road 1900.

The Little Naches River Basin: Roads and Timber Harvest, 1930s-1990s

The landscape of the Little Naches River basin began to change with the graveling (1929) and paving (1934) of Road 1900 road for 9.7 km upstream of the mouth. This was the primary road until 1962, when increased timber harvest activity initiated the construction of new roads. From the turn of the century to 1962, there were only 32 to 48 km of primary and secondary roads throughout the basin. Between 1962 and 1990, 483 km of roads were constructed. Road densities in different watersheds in 1990 ranged from 2.6 to 8 km/km² (Ehinger, Naches Ranger District, pers. comm.). Recreational pressures increased with the construction of new roads.

Riparian areas near roads became popular in the 1950s and continue to be significant sites of recreational activity. Camping with vehicles and off-road equipment reduced riparian understory vegetation and rooting strength, and caused soil erosion and compaction near stream banks and trail and road crossings. Stream and riparian habitats also exhibit modifications of riprap and other channelization practices that protect campgrounds from stream flows and processes of erosion and deposition.

A unique aspect of the Little Naches land-use history is the relatively late entry of timber harvesting compared with earlier harvest activities in western Washington. The basin was fairly isolated, and access from the Yakima Valley was difficult, partly because of steep landforms in the Horseshoe Bend area of the Naches River (Gossett 1979). Prior to the late 1950s, harvest was limited to extracting large trees from the lower valley bottoms and adjacent slopes. Most of the timber was used for building local homesteads, fences, mining and trapping cabins, boxes and palettes for orchards, and firewood. Initially, trees were removed mostly by horse and wagons or by floating them down the river. There are no records of the amount or location of timber harvested prior to the creation of the Washington Forest Reserve.

Truck logging began in 1931 after the road through the Horseshoe Bend improved access to the Naches valley. Most of the private timber land

in river valleys outside the Forest Reserve was completely logged by 1944. Truck logging created the need for road improvements. Through the 1970s selective timber harvests were extended throughout the Little Naches River valley and portions of downstream tributaries. Between 1963 and 1975, 17% of the harvestable acres of the basin were harvested. Commercial thinning was initiated in dense forest stands around 1975.

In 1975 the first timber clear-cuts appeared in lower portions of the Little Naches River basin. From 1975 to 1985 clear and partial cuts extended throughout the basin, including the headwater areas of the South Fork, Middle Fork, Sand Creek, and Matthew Creek. Clear-cuts on private land holdings in the headwaters were also initiated in 1975. About 26% percent of the harvestable acres in the basin were harvested by 1985, 32% by 1990, and 35% by 1992. Potential long-term impacts of these timber harvest activities (1935-1992) near streams and riparian areas of the Little Naches River appear as chronically eroded areas on aerial photos (Smith 1993).

The Little Naches River: Changes in Stream Habitats, 1935-1992

The mainstem of the river extends ~21.2 km upstream from its confluence with the American River to the confluence of the Middle and North Forks. The valley alternates between narrow and wide reaches, with the lower end being more constrained between basalt slopes and upstream areas containing reaches with wide alluvial valleys. Most of the basin lies within the Wenatchee National Forest, with portions of the headwaters under checkerboard ownership by Plum Creek Timber Co.

From 1990-1992 the Pacific Northwest Research Station (USFS), in cooperation with the University of Washington and the Wenatchee National Forest, resurveyed over 80 km of historically surveyed (US Bureau of Fisheries, 1930s and 40s) tributaries in the Yakima River drainage. The resurveys, which include the Little Naches River, Rattlesnake Creek, and the American River of the Naches River Basin, showed minor increases in pool habitats in both managed and unmanaged portions of the Yakima River Basin (Smith 1993, McIntosh *et al.* 1994b). Over the same period, the dominant substrate size changed from gravel to coarser rubble and fine particles in the Little Naches River.

The objectives of resurveys in the Little Naches River basin were to assess changes in pool habitats and substrate size composition between 1935 and 1990 (Smith 1993). The 1990 resurveys show the frequency of large pools increased from 1.7 to 4.6 pools/km. Significant changes also occurred in gravel, fine, and coarse-sized substrate particles. For the mainstem channel, the percentage of spawning-size gravel declined by 50% while fine sediments (>6 mm) increased by 6%. The increase in fine sediments corresponds with the apparent high embeddedness of fines within larger substrates (~15% to 30% of the 20-km mainstem). The compaction or embeddedness of large substrates with fine sediments can change channel and erosive conditions during different stream flow levels (Beschta and Platts 1986), for example, the effectiveness of moderate discharge levels to transport gravels (Lisle 1982). Potential long-term effects in the Little Naches River appear as reductions in gravels and spawning areas for salmon.

The 1990 survey indicated that the majority of pools were bedform scour pools controlled by large substrate and bedrock. These large substrates represent the major roughness elements in the channels because of past removal of logs by the Forest Service and potential low inputs of wood from riparian areas (Smith 1993). These results and observations of the 1935 survey, suggest that large pool habitats were naturally sparse or had been degraded by human disturbance prior to 1935. By 1990, large substrates or boulders increased significantly, comprising almost 50% of the stream bottom substrates. Many of the pools in 1990 were in the constrained reaches of the Little Naches River, where larger boulders and exposed bedrock permitted scouring of smaller particles and the formation of more frequent and larger pools. Greater confinement of 80% of the main channel by road and riprap construction also increased stream energy, magnifying the effects of scour at high flows and the displacement of smaller particles.

The Little Naches River: Changes in Riparian Habitats, 1949-1985

A retrospective analysis of changing riparian conditions using historical aerial photos (Smith 1993) included the lower and upper mainstems of the Little Naches River. Grazing, fires, roads, recreation,

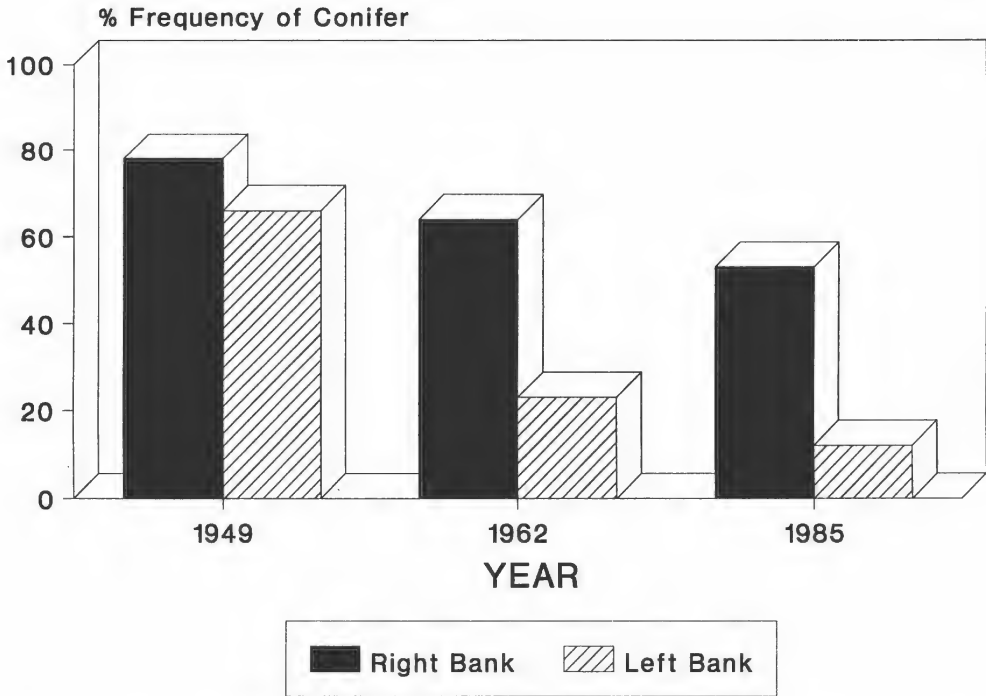


Figure 2. Percentage of riparian area in conifer vegetation along the lower mainstem of the Little Naches River, WA. Left and right banks are assigned in downstream direction. Data collected from aerial photos and expressed as percent of the channel length for the lower mainstem (Smith 1993).

and timber harvest impact these areas differently because of differences in valley geomorphology and the timing of resource use. The lower mainstem (~ 12 km of channel) is naturally constrained by basalt bluffs, with riparian vegetation being limited to small areas along the channel. The most dramatic changes for the lower mainstem occurred between 1949 and 1985 on the left side (looking downstream) of the river. The percent conifer area decreased from 66% in 1949 to 23% in 1962 and 12% in 1985 (Figure 2). In these riparian assemblages, the proportion of mature and old growth trees decreased from 67% in 1949 to 13% in 1962 and then 50% in 1985. The conifer forest was replaced by unvegetated ground (28% to 56%) (Figure 3), with some mixed conifer and deciduous trees still present. On the right side of the river, the decline in conifers was less dramatic (78% to 53%). Here, the proportion of mature and old-growth areas decreased from 56% in 1949 to 14% in 1962, followed by an increase of 37% in 1985. Conifers were replaced by a young, mixed forest.

The reduction in conifer stands, increases in unvegetated areas, and riparian canopy openings adjacent to the stream channels (Figure 4) suggest the combined impacts of different resource uses and natural disturbances. The most apparent impacts include selective harvest in the 1960s, floods in 1964 and 1977, increased recreational use, highway construction, and the placing of riprap along the main channel. For the lower mainstem, the mean width of riparian canopy opening during the last 40 yrs increased from 36 m in 1949 to 67 m in 1985 (Figure 4). During this period the mean active channel width remained constant at 20 m (Figure 4).

The upper mainstem (~8 km of channel) is less constricted than the downstream channel and meanders through large, open alluvial valleys with well-developed soils and riparian areas. Here, the degradation of riparian vegetation and stream habitats by grazing tended to persist through the early 1940s. During the following 20 to 35 yrs,

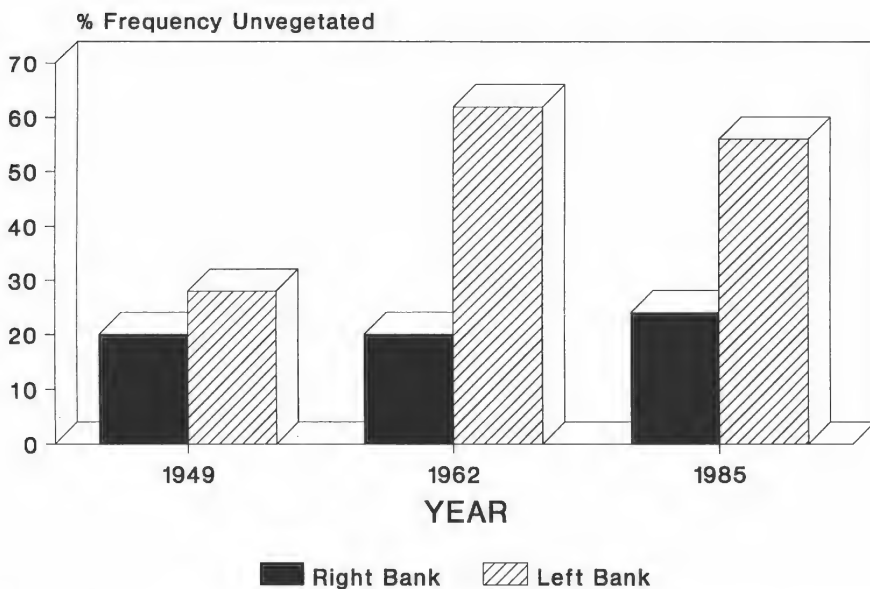


Figure 3. Percentage of unvegetated riparian area along the lower mainstem of the Little Naches River, WA. Left and right banks are assigned in downstream direction. Data collected from aerial photos and expressed as percent of the channel length for the lower mainstem (Smith 1993).

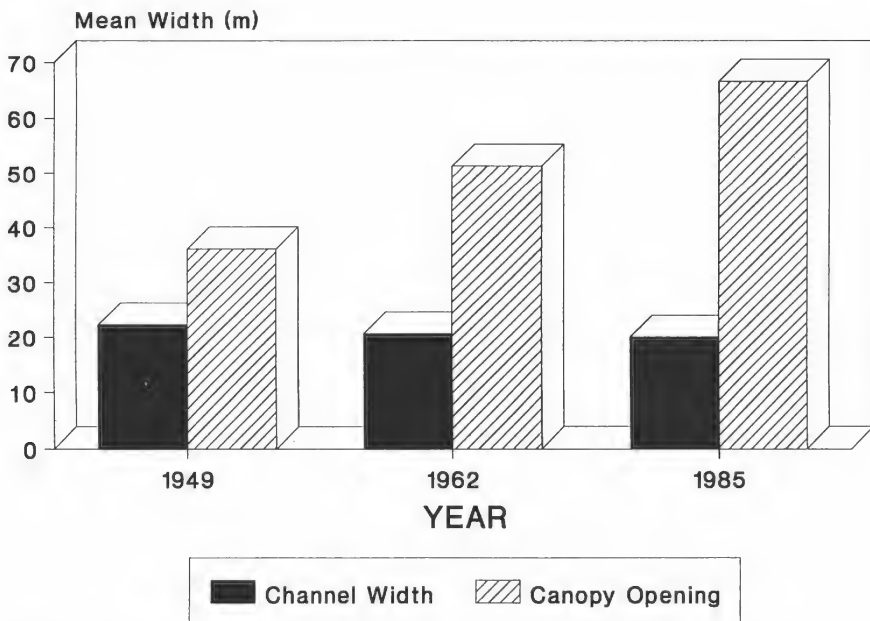


Figure 4. Mean active channel width and canopy opening width of the lower mainstem Little Naches River, WA. Active channel width is defined as the proportion of the channel bottom influenced by bedload transport. Data is from aerial photos (Smith 1993) with channel and canopy opening widths in meters (m).

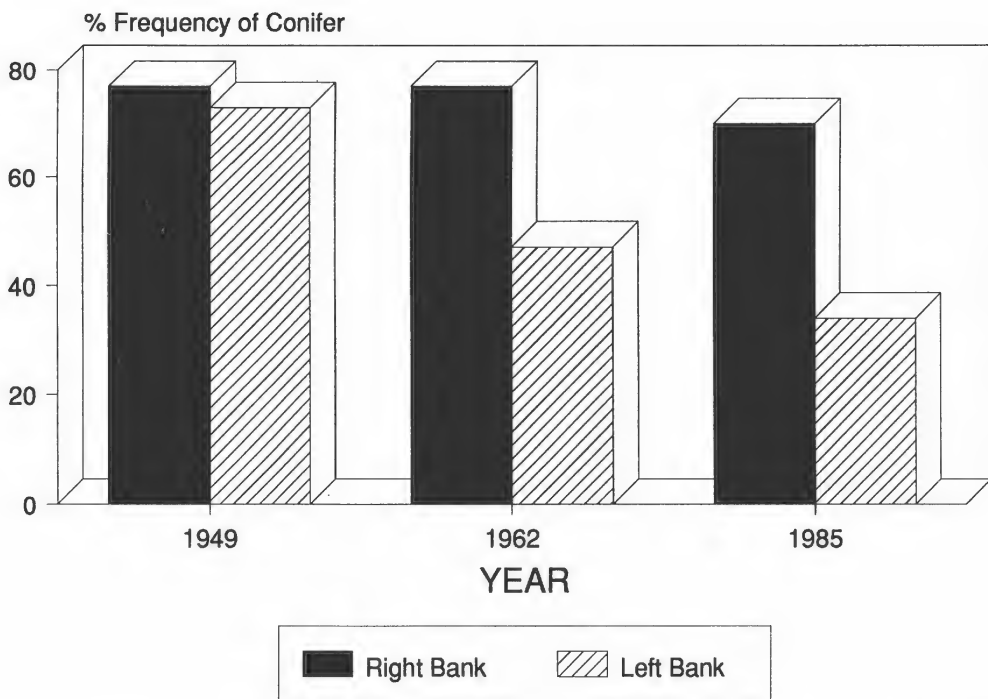


Figure 5. Percentage of riparian area in conifer vegetation along the upper mainstem of the Little Naches River, WA. Left and right banks are assigned in downstream direction. Data collected from aerial photos and expressed as percent of the channel length for the upper mainstem (Smith 1993).

there was a hiatus from intensive land-use disturbance, permitting riparian vegetation to grow and mature. In 1985 the riparian vegetation on both the left and right banks was still dominated by conifers (34% to 70%), but the age groups had shifted from old and mature trees to young and small trees. Conifers decreased over 50% on the left bank because of construction of the main road through the riparian area (Figure 5).

Between 1949 and 1962, both the mean widths of the riparian canopy opening and active channel for the upper mainstem decreased ~30% (Figure 6). The decreased riparian widths of the upper mainstem contrast with the increased widths of the downstream mainstem. Between 1962 and 1985, no detectable changes occurred in the upper valley, which is partially explained by the delay in timber harvest until 1975 and the minimal impact of two large floods in 1964 and 1977. Cumulative effects of timber harvest and road construction were not evident in the aerial photo records.

The environmental history for channel and riparian areas of the Little Naches River suggests large portions of the riparian areas lack the capacity to buffer streams from land-use impacts over the next decade. Retrospective observations show decreases in mature conifers, increases in unvegetated areas, and wider canopy openings. These changes indicate a lower capacity of riparian areas to provide inputs of large wood to channels and protect streams from land uses that cause stream-bank erosion and elevated levels of fine sediments, substrate embeddedness, and water temperatures (Ehinger 1990). Although the long-term observations suggest some increase in large pool frequency, most habitat components critical to abundant and healthy fish spawning and rearing habitats declined over the last 55 yrs. Without proper management and protection, these habitat conditions could degrade further with future timber harvest levels and recreational pressures.

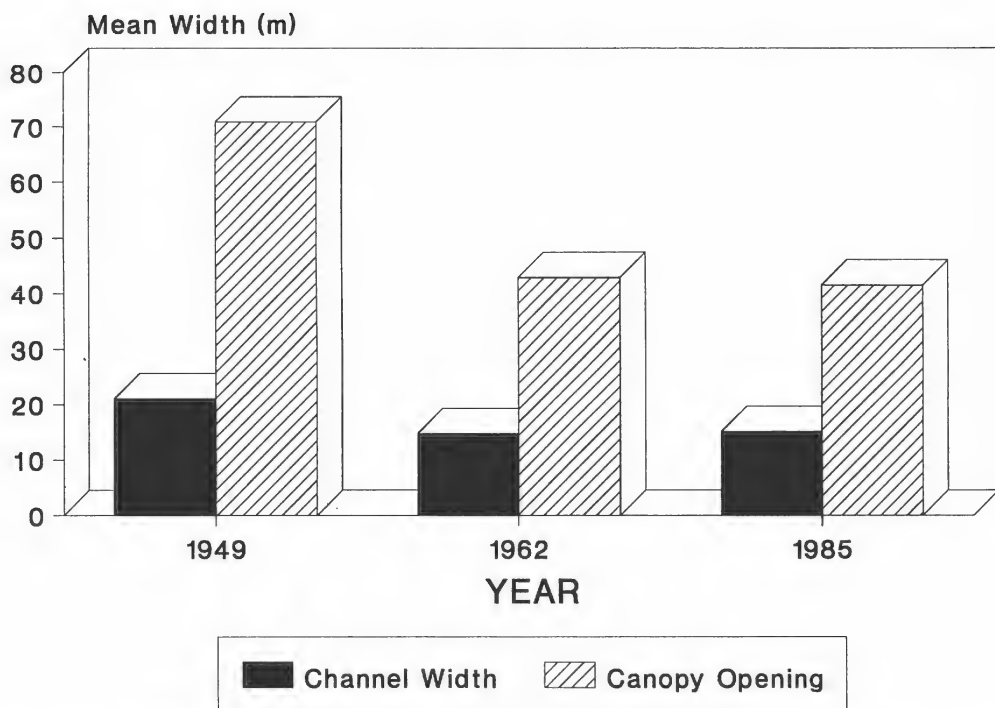


Figure 6. Mean active channel width (m) and canopy opening width (m) in the upper mainstem Little Naches River, WA. Active channel width is defined as the proportion of the channel bottom influenced by bedload transport. Data is from aerial photos (Smith 1993) with channel and canopy opening widths in meters (m).

Upper Grande Ronde River (Eastern Oregon)

Land Uses and Changes in Stream Habitats

In 1990 the Pacific Northwest Research Station (PNW) conducted stream surveys to examine how anadromous fish habitat had changed over time in the Upper Grande Ronde River basin by repeating surveys originally conducted in 1941 by the US Bureau of Fisheries (Rich 1948, Parkhurst 1950). The 1941 survey of the upper basin suggested considerable impacts of land-use disturbances on stream habitats (McIntosh 1992). The 1990 resurvey show a continual disturbance with a >60% loss in mean large pool habitat density. Between 1941 and 1990 pool habitats declined (6.1 to 2.1 pools/km) and fine sediment levels increased throughout chinook salmon spawning areas (McIntosh *et al.* 1994b). Complementary PNW resurveys of wilderness streams (1990-92) throughout the Columbia River Basin have shown that mean large pool habitat density increased

(from 3.9 to 6.9 pools/km) over the 50-yr period (Sedell and Everest 1990, McIntosh *et al.* 1994b).

The changes in the Upper Grande Ronde River Basin since 1941 suggest that the cumulative effects of land-use have caused extreme degradation of stream and riparian habitats across the entire riverine landscape. The loss of pool habitats indicates fewer rearing areas for juvenile fish and resting habitats for adult fish prior to spawning. The reduction in pools also points to minimal refugia, which enable adults and juveniles to avoid catastrophic events like floods, ice flows, droughts, and fires (Sedell *et al.* 1990). The loss of habitat complexity, along with poor substrate and water temperature conditions, also tends to cause fish to crowd into smaller spaces and be increasingly susceptible to disease, competition, and predation.

The 1990 stream resurveys indicated that fine sediment levels were high throughout the headwaters of the Upper Grande Ronde River. Current fine sediment conditions are well in excess of levels

recognized as consistently reducing egg survivability (> 20% surface fines; Bjornn and Reiser 1991). Past studies have demonstrated the detrimental effect of fine sediments on salmonid reproduction (Everest *et al.* 1987, Chapman 1988). The presence of excessive levels of fine substrates limits the quantity and extent of spawning habitat as well as summer and winter cover for juvenile fish and other ecosystem functions (Meehan 1991).

Both the loss of pool habitat and problems of highly degraded riparian habitat and extreme water temperatures in the Upper Grande Ronde River Basin (James 1984, Oregon Dept. Fish and Wildlife 1987, Northwest Power Planning Council 1990, Wallowa-Whitman National Forest 1990) suggest that anadromous fish habitat remains in critical condition. Forest Service stream surveys in 1990 indicate that habitats in over 70% of the stream miles in the Upper Grande Ronde River Basin fail to meet desired Forest Plan stream standards for fine sediments, stream shading, large wood debris densities, and water temperatures. The extremely low return of adults (1990 estimates of < 100 fish) in the Upper Grande Ronde suggests that poor habitat conditions, along with high levels of mortality at mainstem dams, have contributed significantly to the depressed spring chinook runs (J. Zakel, Oregon Dep. Fish Wildl., Salem, pers. comm.). The Upper Grande Ronde represents a primary spawning area for the spring chinook, currently listed as threatened in the Snake River drainage under the Endangered Species Act.

Historic land-use records indicate that domestic livestock grazing, splash dams and associated log drives, along with mining, significantly impacted anadromous fish habitat and streamflows prior to 1941. Stream channelization, due to the availability of heavy equipment after World War II, also greatly reduced stream habitat diversity throughout many portions of the Upper Grande Ronde. Timber harvest and road construction have increased substantially since the 1950s, becoming the dominant land-use activities in the Upper Grande Ronde River basin. The legacy of historic land uses, coupled with the impacts of current upslope management practices, is pervasive and continues to forestall the recovery of stream habitats (McIntosh 1992, McIntosh *et al.*, 1994b).

Land-Uses and Changes in Streamflows

Analysis of long-term streamflow and climate records for the Upper Grande Ronde River indi-

cates significant changes in these parameters since 1904. Streamflow records show a near doubling in the summer base flow (~3% the annual water yield). However, during this period precipitation levels declined, suggesting factors other than climate change influence base flows. The increased base flows appear related to past insect infestations and timber harvest, which removed tree canopies. The loss of forest canopy area reduces water loss through evapotranspiration (Sidle *et al.* 1985). The result is more water being retained in soils and available for release to streams through subsurface flows. However, the higher base flows did not translate into increased annual discharges (McIntosh 1992).

The high level of harvest in the Upper Grande Ronde River Basin since the 1930s may have caused the timing of snow melt and peak discharge rates to shift to about 1 mo earlier in the year. Hydrologic studies in Oregon show greater snowfall accumulations in the clear-cuts, which melt earlier with increased exposure to solar radiation (Harr 1983). In eastern Oregon, earlier snowmelt and peakflows reduce water storage in surface and subsurface areas of channels and floodplains, which can lead to lower annual discharge and instream flows available for stream habitats (Elmore and Beschta 1987, Sedell and Beschta 1991).

The earlier peakflows may also influence the survival of salmon smolts because fish outmigration, which involves a critical physiological phase in salmon life history, is timed largely to peak flows (McIntosh 1992). Early peakflows could force smolts to outmigrate prior to the smoltification and lower fish survival.

Restoration Efforts

Restoration of stream and riparian habitat in the Upper Grande Ronde River basin will require fundamental changes in upland and riparian management practices and a long-term commitment to scientifically based and biologically credible ecosystem management. A framework has been developed in the Upper Grande Ronde River Anadromous Fish Habitat Protection, Restoration, and Monitoring Plan (Anderson *et al.* 1992). Protection of the best habitat along with restoration of historic habitat should be the long-term objective. In the short-term, anadromous fish stocks need relief from highly unfavorable rearing and spawning conditions. This may best be accomplished through protection and restoration of these critical habitats

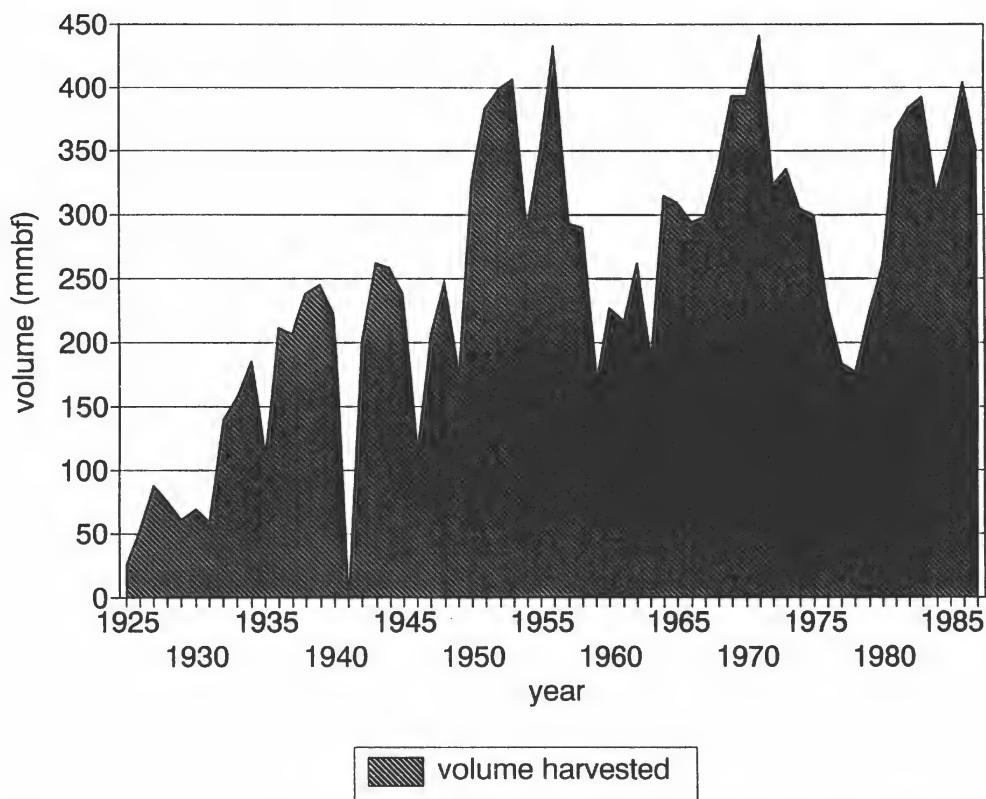


Figure 7. Volume of timber harvested in the John Day River basin, 1925–1990 (Oregon Department of Forestry 1990). Harvest levels expressed as million board feet (mmbf).

by facilitating increased streamflows and reconnecting stream reaches and adjoining refuge area reaches.

Historical analyses of the Upper Grande Ronde River land- and water-use impacts on stream and riparian habitats and other river basins of eastern Washington and Oregon (McIntosh *et al.* 1994b) provide useful time frames for identifying desired future conditions and opportunities for restoration. Stream and riparian habitats have variable distributions in different river basins because their ecological functions depend on influences of several environmental conditions. In the Upper Grande Ronde River, as in other river basins, the development of riparian and stream habitats over time varies with climate, landform, and hydrology. An important landscape factor includes unconstrained reaches

where stream and riparian habitats are highly connected (Gregory *et al.* 1989, Lamberti *et al.* 1989, Moore and Gregory 1989). The importance of unconstrained reaches in the Upper Grande Ronde River basin is evident in the distribution of pool habitats. Most of the pool habitat, both in 1941 and 1990, occurred in unconstrained reaches in wider valleys with floodplains. In 1941 the unconstrained channel reaches, while comprising 40% of the total stream length, contained 69% of the pool habitat. By 1990 the same reaches held only 48% of the pool habitat. The historic trends for stream and riparian habitats in the Upper Grande Ronde River basin indicate management efforts should be focused on improving habitats in unconstrained reaches. These areas commonly exhibit fluvial and geomorphic characteristics that favor habitat development and faster rates of recovery.

John Day River (North Central Oregon)

Early Settlement and Land Uses

Historical accounts of the John Day River describe its streambanks as covered with dense growths of aspen, poplar, and willow. Anecdotal reports, such as the inability of Peter Skene Ogden, a fur trader during the 1820s, to ford horses across the river near the town of Prairie City during summer low flows, suggest that the hydrograph has changed substantially (Hudson Bay Historical Society 1950). Beaver were also reported to be very abundant. Historical photographs of the river at Picture Gorge show cottonwood galleries a quarter mile wide where only a few trees now exist (Bancroft Library, Univ. California, Berkeley). Prior to settlement, the basin supported substantial runs of spring and fall chinook salmon and steelhead and resident fish such as bull trout (*Salvelinus confluentus*, Ratliff and Howell 1992). Currently salmon runs are suppressed, with fall chinook being nearly extinct (escapements < 100 fish; Errol Claire, ODFW, John Day, Oregon) while spring chinook runs range from 2,000 to 5,000 and steelhead from 15,000 to 40,000 fish (Northwest Power Planning Council 1989).

The first settlement in the basin came when gold was discovered in 1862. Most of the mining occurred in the upper mainstem of the John Day near Canyon City, the Middle Fork of the John Day near Galena, and the North Fork of the John Day near Sumpter, Oregon. Placer mining and, later, dredge mining drastically changed the character of the landscape. Dredging disturbed riparian vegetation, overturned bottom substrates, channelized streams, and devastated spawning gravels with the deposition of fine sediments. The legacy of this period remains today, with many kilometers of dredge spoils adjacent to stream channels and retarding riparian plant development. Dredge deposits are especially evident along the North and Middle Forks of the John Day, and settling ponds in the upper North Fork remain a source of toxic heavy metals (Hudson Bay Historical Society 1950). Streamflow in several creeks in the Malheur National Forest goes subsurface because of streambed disruption and substrate aggradation.

During this early period, irrigation and logging began. The first sawmill was established in 1862 (Oregon Water Resources Department 1986). Cattle grazing operations began during the 1860s, primarily near Lower Rock Creek and the towns

of Clarno and Shaniko. Sheep were introduced in the 1880s, and by the 1900s, when the railroad was established, Shaniko became one of the world's largest shipping centers of wool. Early photographs show the hillsides so thick with sheep that on first glance it appears as if they are snow drifts (Oregon Historical Society, Portland, Oregon). Throughout this period, grazing intensity was high. For example, Alder Creek, a small watershed of 89 km², had heavy grazing by 30,000 sheep over a few years. Soon after sheep were introduced, cattle followed. The introduction of exotic herbivores was especially damaging as the vegetation of eastern Oregon and Washington evolved without large, grazing herbivores (Mack and Thompson 1982). The native bunchgrasses were decimated, and exotic flora such as cheatgrass became established.

Prior to the settlement by Euro-Americans, fire return intervals ranged from 45 to 75 years in Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) communities and 10-15 years in mountain big sagebrush (*Artemisia tridentata vaseyana*)-ponderosa pine (*Pinus ponderosa*) associations (J. Boone Kauffman, Dept. Rangeland Resources, Oregon State Univ., pers. comm.). Grazing, fire suppression, and the introduction of exotic plants have greatly altered plant community composition and disturbance cycles. Natural fire cycles have been disrupted, thereby changing nutrient cycling and patterns of plant succession. The present plant communities bear little resemblance to the original flora. These changes undoubtedly have altered the natural hydrologic cycle.

Native plant communities changed as a result of the expansion of western juniper (*Juniperus occidentalis*) and sagebrush, and exotic plants, including those not palatable as forage, began to crowd out native bunchgrasses. The present plant communities are less subject to the low intensity range fires of the past, which reinforces the present plant assemblage structure (J. Boone Kauffman, Dept. Rangeland Resources, Oregon State Univ., pers. comm.). The expansion of juniper is especially noticeable when comparing historic and recent photographs of specific locations. For instance, aerial photographs taken of the area surrounding the cities of John Day and Canyon City show that juniper were confined to small pockets in 1939 (Oregon Water Resources Department 1986). Photographs taken in 1986 show that junipers now dominate the landscape. Western juniper can intercept and transpire as much as 25% of the

precipitation. Junipers in central Oregon range from 460 to 1040 trees/ha. Estimates indicate that for a 161,880 ha watershed, with 618 junipers/ha, water lost through transpiration could be equivalent to 99 to 212 m³/sec/day (J.R. Sedell, Pac. Northw. Res. Sta., Corvallis, Oregon, pers. comm.).

The Blue Mountain Forest Reserve was established in 1906, and by the 1920s timber harvest had become an important activity in the basin. Currently, timber harvest is the major land-use activity on the Ochoco, Umatilla, and Malheur national forests. The historical record indicates that timber harvest steadily increased until about 1950 and has remained at these increased levels to the present (Figure 7).

Changes in Stream and Riparian Habitat Conditions

The combined impacts of all human activities have dramatically changed the riverine landscape of the John Day basin. The hydrograph has changed significantly, with base flows increasing in all managed watersheds and remaining the same in the wilderness drainage. This suggests that the land (e.g., riparian habitats) has lost the capacity to store water for release during the low flow periods of summer (McIntosh *et al.* 1994b).

Hydrologic changes are also implied by the more frequent and severe flash floods and their subsequent impacts. Recent research suggests that the impacts of flash flooding are far more deleterious on fish communities in highly altered stream reaches than those in more natural conditions (Pearsons *et al.* 1992). Turbidity in some parts of the basin, such as Cottonwood Creek, a tributary to the North Fork, is notoriously high after storm events. The resulting siltation of stream beds decreases aquatic insect production and degrades spawning gravels.

The riparian canopy is completely gone in many parts of the John Day River basin, with less stream cover and shading than the recommended 75% closure. A study of several small tributary streams indicated the impact to riparian vegetation and stream water temperatures can be quite severe where the riparian habitat has been altered through activities such as grazing (Pearsons *et al.* 1992). Frequently there is insufficient cover, increased water temperature, and minimal cold-water refugia in river channels of the region (Berman and Quinn 1991, Rhodes and McCullough in press).

Severe increases in water temperatures, both summer and winter, are critical limiting factors for salmonids over many portions of the John Day River basin (Adams *et al.* in press, Li *et al.* 1992, Li *et al.* in press). Tiedemann and Higgins (1989) found that the short-term threshold for rainbow trout (23.8°C), as recommended by the US Environmental Protection Agency, was regularly exceeded in streams where experimental grazing was tested. However, they did not attribute this to grazing practices. Li *et al.* (in press) found that daily temperatures regularly exceeded the upper incipient lethal temperature (26.5°C, Bidgood and Berst 1969) for steelhead trout in Rock, Mountain, and Alder creeks. These tributary streams of the John Day River have been highly impacted by cattle grazing.

Hypotheses have been advanced that the inland rainbow trout populations of the John Day Basin are more adaptable to higher temperatures than other strains. However, Li *et al.* (1992) found that rainbow trout selected coldwater habitats when the ambient temperature of the main stream approached 24°C. Interestingly, rainbow trout were rarely in cold-water habitats when the stream temperature was below 20°C. Li *et al.* (1992) suggest that unless maps of temperature microhabitats are described, the inference concerning temperature adaptability of inland rainbow trout may be misleading.

High temperatures can have several different impacts in stream ecosystems. Fish can be subject to lethal and sublethal thermal stresses that impose severe metabolic costs. In the John Day basin, some stream reaches that exceed 32°C during the diel cycle in the summer are devoid of all fish (Li *et al.* in press). Studies for the John Day using the metabolic model of Wurtsbaugh and Davis (1977) suggest that the metabolic maintenance demand by juvenile steelhead increased 23% to 43% from the coolest to the warmest stream reaches (Li *et al.* 1992, in press). Spring chinook in the John Day River may be even more affected by high temperatures. The optimal temperature range for juvenile spring chinook is 7.9-13.8°C (Reiser and Bjorn 1979) and the upper incipient lethal temperature is near 25°C (Brett 1952).

The lack of thermal cover by riparian ecosystems in the John Day Basin also appears to impact fish food webs. Higher solar radiation levels at stream surfaces and benthic algal production can

induce or alter the development of prey types that may or may not be available as fish food (Tait *et al.* 1994). For example, in the John Day basin standing crops of algae become higher in exposed reaches (no riparian cover) of streams owing to light enhancement of primary production. However, the increased algal forage base for aquatic insects did not translate into greater prey availability for the fishes. The algae supported additional invertebrate biomass comprised of large, stone-cased caddisflies, *Dicosmoecus gilvipes*, whose protective cases rendered them invulnerable to predation by fish.

Stream and Riparian Habitat Rehabilitation

Stream and riparian ecosystems of the John Day and other eastern Oregon watersheds have suffered from poor livestock and forestry practices (Kauffman and Krueger 1984, Kauffman 1988, Beschta *et al.* 1991). Although most of the evidence is anecdotal, conventional wisdom holds that the carrying capacities of these streams for salmonids have been greatly diminished. As a result, large sums of money have been invested in habitat restoration in eastern Oregon as part of the long-term plan to restore anadromous salmonids in the Columbia River System. For example, the Bonneville Power Administration (BPA) spent ~\$6,000,000 in the John Day basin (Rick Stoots, Bonneville Power Admin., pers. comm.). Unfortunately, no funds were allocated for monitoring projects because evaluation was not considered in the design of restoration work. The result of this policy is that the degree of effectiveness of various restoration efforts is unknown.

Three evaluation studies of habitat rehabilitation efforts have been conducted under the adverse circumstances of having no available monitoring data from before or after implementation of enhancement projects. These evaluations include (a) a bio-economic study of habitat restoration (Adams *et al.* in press), (b) a study of log sill/log weir emplacements in Camp Creek of the John Day basin (Li *et al.* 1992), and (c) a field review of stream enhancement projects in eastern Oregon (Beschta *et al.* 1991). Adams *et al.* (in press) found that different stream factors limited the capacity of habitats in different physiographic settings. They suggested that increased summer streamflow and reduced temperatures could increase fish use of habitats. Li *et al.* (1992) found that installation of log weirs in Camp Creek did not address the criti-

cal problem of water temperature, the major limiting factor in Camp Creek. The objective of the habitat enhancement program was to increase the number of pools in a riffle-dominated system. The effect of installing ~280 log weirs (~\$750 per log weir) was to increase pool volume by 4%. Moreover, increased rainbow trout densities and use of habitats were insignificant.

A visual evaluation of habitat rehabilitation projects was made in the John Day basin. Beschta *et al.* (1991) assessed the status of riparian vegetation development and geomorphic processes in stream channels. The authors concluded that efforts to rehabilitate stream habitat on a site-specific basis without examining the entire river and riparian basin landscape contributed to the failure of many projects. Beschta *et al.* (1991) suggest that the most effective means of restoring habitat is to facilitate natural riparian plant succession and to reduce the most detrimental source of disturbance, livestock grazing. They also suggest that cattle exclosures can be excellent tools for habitat restoration. Hard-structure emplacements in stream channels appeared to create minimal benefits at the cost of disrupting the natural processes of the stream channels and interactions with floodplains

All the above studies indicate that most of the enhancement programs are non-palliative in addressing the basic causes of habitat changes. Furthermore, because of the lack of basic physical and ecological information, current rehabilitation programs could be creating the illusion that habitat restoration can be quickly accomplished through technological means. For enhancement programs to succeed, they need better landscape information about habitat structure and functions. This data can be obtained using long-term monitoring programs. Careful consideration must be given to temporal scales of salmonid life cycles, fish relationships to stream habitat changes and riparian plant succession patterns, and influences of restoration efforts.

Historic Cumulative Impacts of Resource Uses and Management on Stream and Riparian Ecosystems

The case histories for the Okanogan, Methow, Naches, Grande Ronde and John Day River basins show that stream and riparian ecosystems have experienced long-term cumulative impacts by numerous resource uses and management

practices. Continuous impacts and neglect over the past 100-150 yrs have caused considerable habitat damage (Kauffman and Krueger 1984, Kauffman 1988, Elmore and Beschta 1987, Beschta *et al.* 1991). These impacts commonly influence stream and riparian systems at the same time because waters, soils, and plants are connected and function together by exchanging water, sediments, nutrients, and organic matter (Minshall *et al.* 1989, Wissmar and Swanson 1990, Gregory *et al.* 1991, Belt *et al.* 1992, Leonard *et al.* 1992).

Stream and riparian ecosystems of eastern Oregon and Washington have been and are being continuously impacted by erosion, sedimentation, excessive water temperatures, and water losses induced by livestock grazing, forest management practices (e.g., harvest, roads, and fire), water storage and diversion (dams and irrigation), fisheries, mining, and recreation (Meehan 1991, Mullan *et al.* 1992, Peterson *et al.* 1992, National Council of the Paper Industry for Air and Stream Improvement 1992). A summary of the major changes in stream and riparian ecosystems follows:

- a. the loss of riparian soils and narrowing of riparian forest corridors due to forest management, livestock grazing, recreation and other land-uses (Kovalchik 1987, Kauffman 1988, Clark and Gibbons 1991, Kovalchik and Elmore 1991, Elmore 1992, Pearsons *et al.* 1992, Smith 1993, Wissmar *et al.* 1993);
- b. the loss of large wood recruitment and storage in stream channels because of the decline in riparian forest corridors (Bilby and Wasserman 1989, Carlson *et al.* 1990);
- c. increases in summer water temperatures and related stresses on fish and wildlife because of the lack of shading by riparian canopies and shallower sediment-filled stream channels (Corner 1992, Tait *et al.* 1994, Li *et al.* in press, Maloney *et al.* in press);
- d. increases in water pollution due to agriculture and forest chemicals (Norris *et al.* 1991);
- e. the loss of fish spawning and rearing habitats because of sediment embeddedness of streambeds and low streamflows (Beschta and Platts 1986, Corner 1992, Smith 1993, McIntosh *et al.* 1994b);
- f. loss of stream and riparian ecosystem biodiversity through confinement by highways,

railroads, and flood control levees within floodplain areas (Furniss *et al.* 1991, R.W. Beck Associates 1973); and

- g. the total loss of stream and riparian ecosystems because of water removal for storage and diversion projects (Caldwell and Catterson 1992).

The order of importance of the major factors impacting riparian corridors has been estimated for 11 different river basins of eastern Oregon (Hanson 1987): livestock grazing > timber harvest practices > agricultural practices > road construction > flood events (Table 2). Several managerial features were recognized as important contributors to the severity of these impacts, primarily mixed land ownership, overlapping management jurisdictions, and minimal attention to reducing damaged ecosystems. The following sections review the major management activities that have influenced stream and riparian ecosystems in river basins of eastern Washington and Oregon.

Livestock Grazing

As shown by the case histories, livestock grazing began with the arrival of miners and settlers during the second half of the 19th century. Overstocking of the available ranges during the late 1800s and overgrazing in the early 1900s caused widespread damage, altering riparian plant diversity and compacting and eroding soils (Elmore 1992). Changes in stream and riparian habitat structures commonly followed heavy grazing of watersheds because of increases in surface runoff and sedimentation, and decreases in groundwater infiltration (Hibbert 1976, Platts 1981).

The growth of the livestock industry in eastern Washington and Oregon increased the number of animals beyond the area's carrying capacity (Platts 1991). By the 1920s overgrazing of Forest Service lands and drought conditions caused the range to further deteriorate to the extent that Congress passed the Taylor Grazing Act in 1934 to improve public rangelands. A federal report on the status of the condition of these rangelands indicates that ~50% of the Forest Service and BLM rangelands in the western United States were in fair to poor condition based on vegetative potential (Government Accounting Office 1988). In 1985 a similar report for non-federal rangelands in Oregon indicates ~78% of the private lands were also in poor

TABLE 2. Summary of the “major factors affecting riparian areas” in the different river basins of eastern Oregon (Hanson 1987).

River Basin	Grazing	Logging	Roads	Stream channel- ization	Floods	Irrigation	Spraying chemicals	Mining	Agric.	Dams	Natural erosion	Rural devel.	Recreation
Malheur L.	x	x	x		x	x	x		x				
Malheur R.	x	x	x		x	x		x	x				
Owyhee R.	x				x					x			
Goose & Summer L.	x	x	x								x		
Klamath R.	x	x	x		x				x				
Deschutes R.	x	x		x					x		x	x	x
Hood R.	x	x	x				x		x		x		
John Day R.	x	x	x	x	x	x		x	x				
Umatilla R.	x	x		x	x			x	x				
Grande Ronde R.	x	x	x	x	x			x	x				
Powder R.	x	x						x					

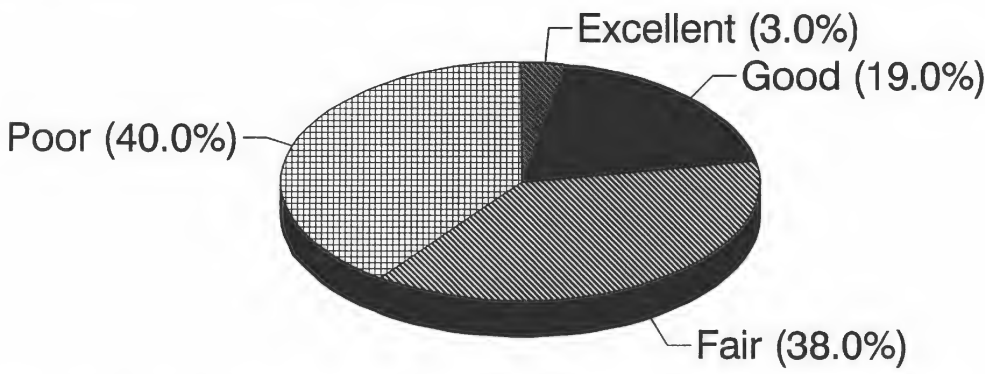


Figure 8. Range conditions of non-federal rangelands in Oregon (Soil Conservation Service 1985). Range conditions expressed as percent excellent, good fair and poor of non-federal rangeland area.

to fair condition based on vegetative capacity (Soil Conservation Service 1985) (Figure 8).

Throughout the 1960s and 70s, the US Forest Service, US Bureau of Land Management, US Soil Conversion Service and private land owners changed grazing practices by using a variety of management strategies. However, minimal attention was given to assessing the impacts of grazing on riparian and stream ecosystems within range allotments (Elmore 1988). For example, while range conditions tended to improve in upland

ranges, minimal gains were observed in riparian and stream areas (Behnke and Raleigh 1978). Other changes in grazing practices, such as the livestock industry’s shift from grazing sheep to cattle, further complicated the situation. Cattle, which prefer to graze in streamside areas, cause considerable deterioration of riparian and stream habitats (Platts 1981, 1991). Alternative grazing strategies have been suggested to protect and restore riparian areas (Elmore and Beschta 1987), but whether different grazing practices can reduce grazing

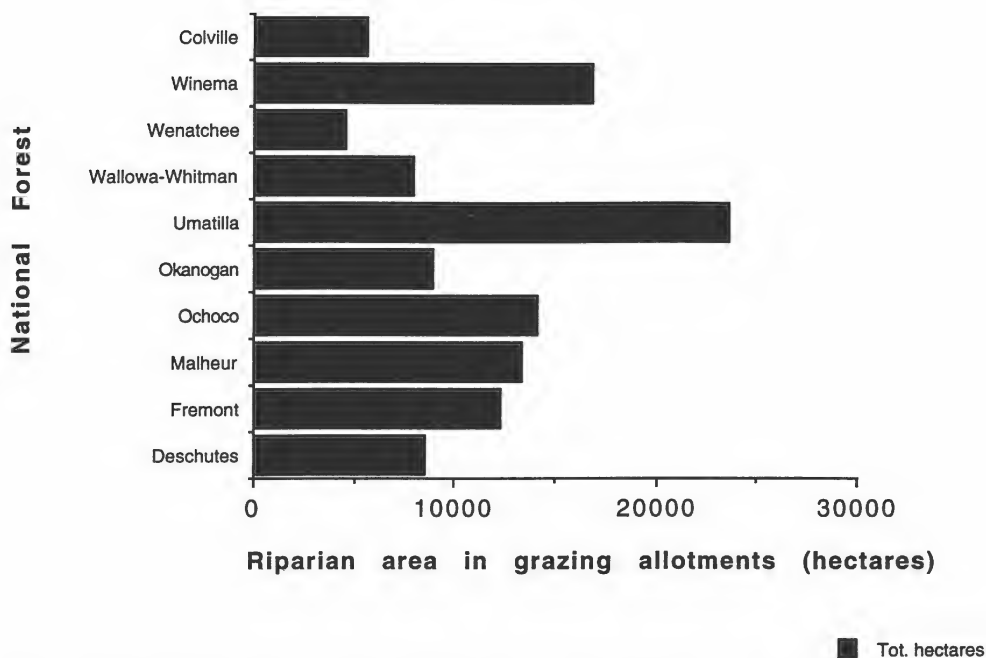


Figure 9. Riparian areas within grazing allotments of National Forests in eastern Washington and Oregon (USDA Forest Service, Region 6, 1992 Range Report, Portland, OR). Riparian area expressed as hectares (ha)

impacts on riparian and stream habitats has not been fully resolved (Rhodes and McCullough in press).

Minimal information exists about the quantity, types, and conditions of riparian ecosystems in eastern Washington and Oregon. The Forest Service recently initiated inventories of riparian ecosystems associated with grazing allotments (Quigley *et al.* 1989, USDA Forest Service Region 6, FY-92 Range Report, Portland, Oregon). Estimates for 10 national forests showed that riparian vegetation areas comprise 4% of the grazing allotments (161,493 ha). The national forests with greatest riparian areas in grazing allotments were the Winema (16,809 ha) and Umatilla (23,620 ha), and those with lowest were the Colville (5,646 ha) and the Wenatchee (4,593 ha) (Figure 9). Although the Forest Service's inventory gives partial estimates of the sizes of riparian areas within allotments, a more extensive program needs to include (a) future management objectives, (b) amounts of riparian acreages adjacent to terrestrial systems, and (c) comparisons of riparian acreages

within allotments with the total riparian acreage of different national forests.

Forest Management and Erosion: Timber Harvest, Roads, and Fire

During the last century and early 1900s, settlers initially harvested forests of eastern Oregon and Washington in river valleys, riparian areas, and adjacent hillslopes using a variety of high grading and other select harvest strategies (Plummer 1902). Harvest records kept by the US Forest Service, Washington Department of Natural Resources (WDNR, 1985), and Oregon Department of Forestry (ODF, 1985) since about 1925 indicate two different patterns of timber harvest in eastern Oregon and Washington (Figure 10). Harvest levels in eastern Oregon increased dramatically prior to and after World War II followed by further increases through the 1950s and 1980s. In contrast, harvest levels in eastern Washington have remained at fairly stable levels since 1925, increasing slightly over the past 65 years. Harvest levels in eastern Washington have been about one-third

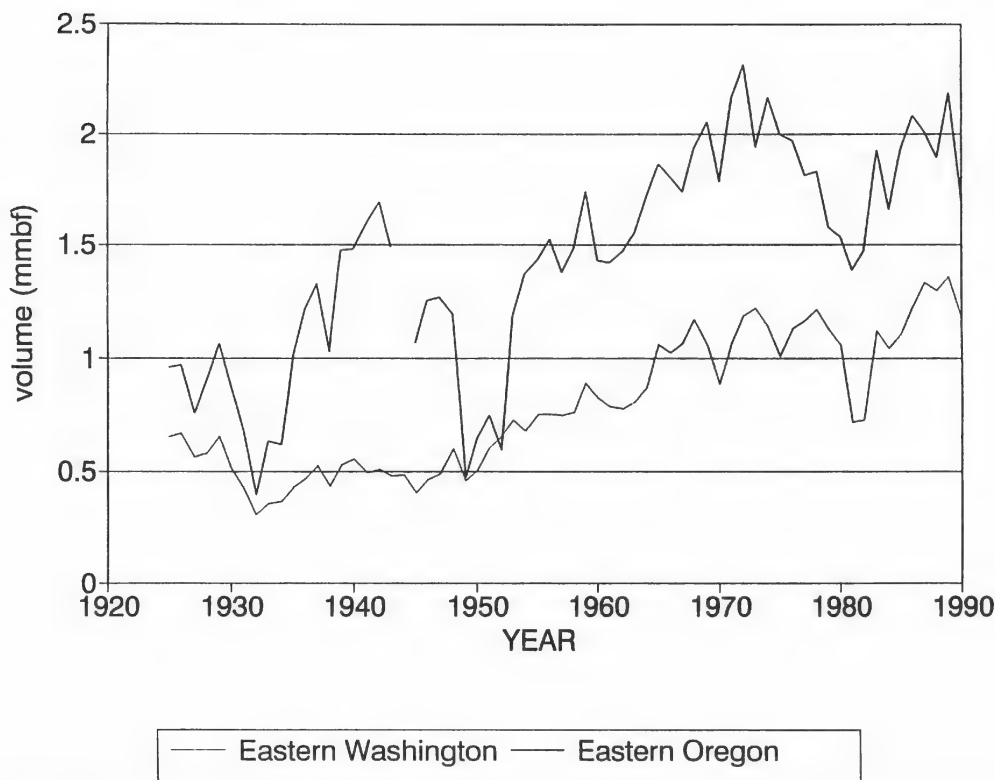


Figure 10. Timber harvest levels in eastern Washington and Oregon, 1925-1985 (Washington Department of Natural Resources 1985, Oregon Department of Forestry 1985). Harvest levels in million board feet (mmbf).

those of eastern Oregon (see also Figure 7, total harvest includes private, state and federal). These differences can be partially attributed to ~65% of the Forest Service lands in eastern Washington being in wilderness and roadless conditions, which reduced the land available for timber harvest activities.

During the past three decades (1970s to 1990s), forest management practices in eastern Oregon and Washington have been required to minimize adverse impacts primarily to water quality by applying site-specific best management practices (BMPs) (MacDonald *et al.* 1991). If adverse impacts occurred, they were usually in violation of Section 319 of the Clean Water Act. However, the cumulative effects of timber harvest and road-related activities (Peterson *et al.* 1992) throughout watersheds received little attention in terms of the susceptibility of streams and riparian areas to runoff related to land-use as well as other disturbances.

Many of the water-related issues pertaining to influences of forest management required the development of several management methods. Some of the important issues were the influences of tree harvest, roads, and fires on (a) de-synchronization or alteration of stream flow regimes, (b) soil compaction and erosion, and (c) altered wetted soil mantle and runoff conditions (Tiedemann *et al.* 1979, Harr 1987). In the following sections, we review management approaches pertaining to hydrologic, soil, and fire conditions.

Hydrologic Effects

Forest managers have assumed that de-synchronization of stream flows caused by different logging practices could benefit soil and water resources (Harr 1987). This viewpoint was based on studies of influences of timber harvest patterns on snow accumulation and melt in several regions

(Halverson and Smith 1974, Troendle and King 1987). However, these findings apply to forested regions outside the Pacific Northwest. Harr (1987) points out that de-synchronization or synchronization of flows depends on how flows combine from different runoff sources and tributaries to produce streamflow regimes in downstream reaches. In reality, because of the lack of information about how flows combine under natural conditions east of the Cascade Mountains, managers have great difficulty in evaluating the influences of logging-induced diversity of forest stands on hydrologic responses (Wasson *et al.* 1992).

In recent studies in northern Idaho, King (1989) has evaluated streamflow responses using Forest Service versions of the equivalent clear-cut area (ECA) method. This method attempts to forecast streamflow responses to vegetation removal by timber harvesting, road building, and fire. The ECA procedure has also been used to develop timber harvest schedules (USDA Forest Service 1974, 1977). ECA timber harvest guidelines have commonly placed limits on expected increases in the monthly streamflow during spring runoff to prevent increases in high flows. However, King (1989) found that short-duration streamflows or high peak flows commonly caused sediment bedload movement and altered stream channel conditions (King 1989). King (1989) recommended that maximum daily streamflows provide better stream protection than monthly increases in streamflow. This study also identified the need of applying guidelines for maximum daily streamflows to smaller headwater streams where large increases in maximum daily streamflows can occur following timber harvest. It should be noted that a major requirement for the improvement of forest management procedures, like the ECA, will be the acquisition of high-quality local streamflow and precipitation records.

Soil Erosion

Soil loss can be viewed as the major response of water and soils to problematic land-use practices. To better manage soil erosion problems, the "Klock" Watershed Cumulative Effects Analysis (KWCEA) Model was adapted (Klock 1985) from the Universal Soil Loss Equation (Slaughter and Aldrich 1989). The model was designed for the assessment of the potential impacts of forest practices in small watersheds (> 4,000 ha) on the east side of the Cascade Mountains. The parameters of

the KWCEA model include site erosivity-energy potential based on precipitation (R), site surface erosion factor (E), slope stability factor (S), hydrologic sensitivity characteristic (H), topographic factor (T), total area of activity (A1), and total area of watershed (A2).

The model provides a condition index or threshold for watershed degradation. The threshold suggests relative cumulative effects and provides risk-rating levels of past, current, and future forest management practices (i.e., harvest and roads) and worst-case conditions (Klock 1985). The model's thresholds only apply after certain levels of degradation have occurred, such as impacts caused by floods. The model has minimal applicability for assessing changes in stream and riparian habitat conditions.

Some of the limiting characteristics of the KWCEA Model include the need for (a) mathematical validation of model behavior, (b) statistical validation of risk values, (c) improved data compilation procedures, and (d) the addition of predictive hydrologic and meteorological information. These shortcomings arise from the model being derived from the Universal Soil Loss Equation (USLE) and subsequent modifications for specific watershed problems on the east side of the Cascade Mountains (Mullan *et al.* 1992).

The USLE and its various versions have been used by management organizations over the past 20 yrs, especially for predicting sheet and rill erosion in agricultural areas (Foster 1987, Slaughter and Aldrich 1989). The procedure was derived from the basic equations of Zingg (1940) for the effect of slope length and steepness on erosion. The USLE is an empirical approach with a lumped model structure that severely limits its potential for improvement and increased accuracy. This "black box" model does not define separate relationships for fundamental hydrologic processes of precipitation, infiltration, runoff, and the basic erosional processes of substrate detachment by raindrop impacts, transport, and deposition.

Soil Compaction

Agencies, such as the US Forest Service and US Bureau of Land Management have also developed procedures for the evaluation of soil compaction caused by timber harvest, road building, and recreational activities. A common assumption has been that soil compaction of 12% of the total

watershed area provides a threshold for detrimental changes in streamflow. The origin of this threshold appears unclear and poorly documented. Review of the relationship between flow increases and soil compaction levels demonstrates major difficulties in using this 12% threshold (Harr *et al.* 1975, 1979; Harr 1980; Harr 1987). Harr (1987) defined a curvilinear relationship between flow increase and the amount of compaction as increasing exponentially with soil compaction. This relationship does not indicate a threshold. Soil compaction of 12% corresponded to a 32% increase in peak flow, indicating considerable adverse impacts in streams. The relationship indicates that different streams with varying channel geomorphologies could be adversely impacted by much lower flows than a 32% increase. These results indicate that the physical characteristics of a particular stream must be considered in order to not arbitrarily set the same level of compaction for all streams. Review of both the soil compaction and erosion management procedures indicates that past management thresholds and guidelines have minimal applicability for assessing changes in stream and riparian habitat conditions. They do not consider streambank and channel geomorphologies, stream channel gradients, and critical particle sizes that relate to hydraulic principles (Grant 1987).

Fire Management

Forests of varying stand structures and landscape patterns in eastern Washington and Oregon have developed under natural fire regimes (i.e., high-intensity crown fires and low-intensity underburns). Because of the dry climate and natural fire history most forest stands tend to be less than 400 years old. Historically, frequent but low intensity fires maintained open stands and favored fire-tolerant species. However, during the past century these conditions have been greatly altered. Fire suppression efforts have altered the natural fire regime and therefore the stand compositions. These forests now contain less fire-tolerant tree species with dense understory vegetation (Mullan *et al.* 1992). High fuel accumulations have caused more intense and destructive fires than in the past. Extensive fires in eastern Washington over the past few decades have frequently been hot fires having substantial effects on forest nutrient status and soil conditions (Grier 1975, Tiedemann *et al.* 1979).

The increased severity of these fires has altered the amounts and qualities of nutrients, sediments,

and organic debris delivered to stream channels. For example, studies of nutrient transfer to streams in eastside forests of Washington and Oregon indicate that organic nitrogen levels about doubled during the first year (Tiedemann *et al.* 1979). The most significant effects of fires on streams and rivers were the increased amounts of surface runoff, sediment, and debris delivered to the channels. Studies of the Entiat River basin in eastern Washington have shown that while streamflows increased following fires, the cumulative effects of rapid snowmelt, high-intensity rainstorms, and the destruction of above- and belowground vegetation have resulted in massive debris torrents (Klock and Helvey 1976). The frequencies of the debris torrents increased to 10 to 28 times greater than before fires (Helvey 1980).

Water Diversion and Quality Problems

Irrigation and related water uses have expanded greatly during the past 25 years in eastern Washington and Oregon. Increased withdrawal of water from dams and wells relates to new types of sprinklers, other irrigation developments and the needs of non-agricultural uses. The availability of water from dams and wells combined with large tracts of inexpensive lands has stimulated out-of-state promotions of developments emphasizing farming, recreation, and retirement. Water uses include rural domestic, stock watering, irrigation, public water supply (municipal and light industrial) and industrial. Of the major water demands, irrigation dominates, with ~10 times more water being withdrawn than for municipal and industrial uses (Highsmith and Kimerling 1979).

Both agricultural and non-agricultural activities have greatly increased water demands on surface and subsurface water supplies. Supply problems, when combined with increased cut-over lands in marginal forests, expanded conversions to cropland, and minimal recharge of groundwaters suggest increases in resource conflicts in the near future because of the lack of water (Dicken and Dicken 1979, National Research Council 1992a). The major regional problems related to water withdrawal for irrigation include water storage and drainage, high water temperatures, pollutants, and low streamflows in smaller drainages.

Water diversion from streams and withdrawal from dams and wells have all served to dewater numerous streams and destroy salmonid habitats

and associated riparian ecosystems. Water diversions have elevated summer water temperature and increased pollution and gas supersaturation problems in both the Snake and Yakima Rivers. Although improved water treatment facilities have been responsible for decreased levels of biochemical oxygen demand (BOD), pollution problems persist because of nonpoint sources of organic and inorganic toxic materials and sediments. Nonpoint sources in most river basins of eastern Washington and Oregon appear dominated by more than 20 million acre feet of irrigation return flows (Highsmith and Kimerling 1979). These management practices create other major drainage problems such as over-irrigation and seepage, increases in soil salinity and altered water quality and storage in floodplains and groundwaters.

Water Storage and Fisheries Impacts on Salmon Runs

In most river basins of eastern Washington and Oregon, the loss and degradation of salmon and steelhead habitat and run sizes was ensured by permanent blockage of riverine channels with dams for hydroelectric power and irrigation. An excellent historical example of the problem was the damming of the Methow River basin. The Methow River was completely blocked from 1912 until the 1930s by a hydroelectric dam at Pateros near the river mouth. The Pateros dam caused the extinction of a coho salmon run and perhaps other salmonids. After the dam's removal, the Methow River was planted with hatchery and trap-released salmon and possibly colonized by straying Columbia River fish. The dams on the Columbia River currently limit fish passage and create other survival problems (e.g., predation and temperature) for Methow fish stocks.

Large Columbia River dams, such as the Chief Joseph and Grand Coulee on the upper Columbia River and the Hells Canyon on the Snake River, were constructed between the 1930s and 60s. These large dams, some without feasible fish passage facilities, inundated rivers, destroying rearing and spawning habitats and lengthening downstream migration time. The stream miles of anadromous fish habitat above of the Bonneville Dam has declined from ~11,700 to ~7,600 miles. Cumulative passage mortality for juvenile fish moving downstream can approach 77% to 96%, while adult passage mortality upstream can

range from 37% to 51% (Northwest Power Planning Council Staff 1986).

Additional losses of upper and lower Columbia River salmon runs have occurred because of mixed-stock ocean fisheries and overfishing of weaker up-river and wild fish stocks. Fish harvest rates in the ocean have been commonly set for the stronger, lower Columbia River fish runs downstream from the Bonneville Dam. These fish runs are stronger because they have received considerable hatchery supplementation. The Mitchell Act (16 USC-750) for hatchery programs in 1949 caused downstream river hatchery production in the 1960s to surpass natural production. This extensive production of hatchery fish along with overfishing of wild and upriver runs, and permanent blockage by large dams has led to the elimination of some fish runs as well as changes in the genetic character of many stocks (Northwest Power Planning Council Staff 1986).

Minimum Instream Flows for Salmon Habitats

Another important historical and contemporary impact on salmon populations and habitats in eastern Oregon and Washington has been the diversion and allocation of stream waters. The Methow River basin provides an excellent example of these water uses (Figure 1). Historically and today, irrigation withdrawals during summer low flow periods have limited salmon production and survival in the river. Current salmon runs include steelhead, spring chinook, summer chinook, fall chinook, and sockeye salmon. Life history characteristics and limiting factors of anadromous fish in the Methow and Okanogan rivers have been documented in the Subbasin Salmon and Steelhead Production Plan (Washington Department of Wildlife *et al.* 1989), Kohn (1987, 1988, 1989), Edson (1990), Meekin (1991), and Langness (1991).

Water diversion and allocation issues in the Methow River basin involve local interest groups (business, agricultural, recreational, environmental) as well as the Methow Valley Irrigation District, Okanogan County, the Yakima Indian Nation (YIN), Colville Confederated Tribes (CCT), US Fish and Wildlife Service (USFWS), Washington State Department of Fisheries (WDF), Washington State Department of Wildlife (WDW) and Washington State Department of Ecology (DOE). DOE is responsible for the review of previously adopted minimum instream flows and the assessment of the

impacts of new water right appropriations on salmon habitat. Since 1983 DOE has used the Instream Flow Incremental Methodology (IFIM) to provide information for minimum instream flows (Bovee 1982, Milhous *et al.* 1976, 1989). The IFIM defines fish habitat in terms of water depth, velocity, substrate, and cover.

Most of the local interest groups have disagreed with the findings of the DOE projects (Caldwell and Catterson 1992). DOE maintains that setting of minimum instream flows preserves fish habitat during low flows. The continuous dissent of the groups has only added to the plight of fish and the lack of water. The major concerns include DOE's assumptions pertaining to (a) where and at what times water is withdrawn, and (b) the fate of water when irrigation ceases (Caldwell and Catterson 1992). Some groups believe that all the water returns back to the river while others disagree. Additional concerns have involved DOE's plans for (a) adopting conservation strategies for agricultural uses; (b) requiring environmental standards for water temperature, water quality, and sediment loads (Caldwell and Catterson 1992); and (c) setting additional minimum instream flows necessary for the incubation of eggs, smolt outmigration, fish passage to spawning grounds, and prevention of fry and juvenile stranding. The Yakima Indian Nation has also caused considerable dissension by requesting moratoriums on new wells in the Methow Valley.

In the Methow River basin, many of the above concerns were discussed in the Environmental Impact Statement for the Early Winters Alpine Winter Sports Study (Okanogan National Forest 1990). The EIS recognized the extreme importance of protecting hydraulic continuity of groundwaters with surface waters (Washington State Water Resources Act 1971, RCW Chapter 90.54) but gave minimal attention to water quality and the productivity of riverine and riparian ecosystems. Because of the high degree of hydraulic continuity between groundwater and surface waters in the Methow Valley (Golder Associates 1991), groundwater flows can reverse directions, causing well levels to vary as flows change in the river channel (GeoEngineers 1990). Such variations in flows could cause extreme water pollution problems when combined with possible impacts of nutrient loadings from agricultural and urban storm runoff, golf course fertilization, waste treatment, and waste disposal (Willms and Kendra 1990).

Extensive valley-floodplains with alluvial geomorphic deposits and groundwater flows like those in the Methow Valley have been shown to be extremely important to the ecology of the river. Floodplains having hydraulic connections with channels can support deep belowground habitats penetrated by riverine animals. These animals and estimates of mass transport of nutrients from flowing groundwater habitats or hyporheic habitats point to the extreme importance of these subsurface waters to the biological productivity of the channel and riparian ecosystems (Stanford and Ward 1988, Wissmar *et al.* in press). These hyporheic systems also serve as refuge for macroinvertebrate communities during time of drought and thermal stress.

Mining Activities

Mining in eastern Washington and Oregon has been based on a great variety of minerals such as gold, silver, copper, nickel, chromium as well as gravel and building stone. Mineral mining activities in areas like the Okanogan and Methow River basins have declined during the past half century because deposits were low grade and dispersed. Nevertheless, cumulative and continuous impacts on stream and riparian ecosystems have occurred because of past mining operations. Past placer and hydraulic (1860s-1900), bucketline dredges (1900-30), and lode mining (after 1900) have caused erosion, released leachates, and altered stream flows, damaging stream and riparian habitats. From the 1860s to 1900, because considerable water was needed for working placer and hydraulic operations, long ditches were constructed to divert large quantities of water to the mining areas. In the Blue Mountains of Oregon, the El Dorado ditch flowed more than 160 km from the headwaters of the Burnt River to the placers at Malheur (Dicken and Dicken 1979). Since water is naturally scarce in most of these upland regions, both the mining operations and water diversions greatly impacted streams and riparian systems. Hydraulic mining pits and scars and dewatered stream channels can still be found in many localities. Excellent histories of the influences of mining and the extraction of minerals on streams and headwater drainages can be found in Nelson *et al.* (1991) and Portman (1993). More recent impacts include cyanide chemical-leach mining for gold from old mine deposits and the excavation of stream channels and floodplains for sand and gravel.

The value of sand, gravel, gypsum, and limestone products extracted in most counties in eastern Washington and Oregon has amounted to several times that of precious metals (Highsmith and Kimerling 1979, Wilson 1990). Practices such as mining of river bed gravels deposits within the wetted perimeter of a river using dredges, bulldozers, and front-end loaders can be detrimental to salmonid habitats (Rivier and Sequier 1985, Pauley *et al.* 1989). Altered habitat conditions include changes in (a) shapes, depths, flow patterns, and bottom substrate compositions of channels, and (b) levels of suspended sediments and temperatures in waters (Wydoski and Helm 1980, Rivier and Sequier 1985, Carling 1987). These physical changes can adversely impact fish feeding and migration behaviors, population levels, and available habitats for fish and macroinvertebrate communities (Binns and Eisermann 1972, Etnier 1972, Milner *et al.* 1981, Moore and Gregory 1988, Bjornn and Reiser 1991).

Conclusions

As shown by this document, historic cumulative effects caused by man's use and management of land and water resources over the past two centuries are greatly altering the health of river basins in eastern Oregon and Washington. Past effects on the environment resulting from individual and cumulative impacts of livestock grazing, management of forests, water storage and allocation, agriculture, road construction, flood control, and mining become collectively significant over long time periods and are continuing to occur today. By documenting past disturbances and actions of human institutions that alter ecosystems, we hope this environmental history will provide valuable baselines for referencing and evaluating past and future management criteria.

In eastern Oregon and Washington, histories of land and water management activities in select river basins show minimal actions for reducing damage to stream and riparian ecosystems. Management institutions commonly perpetuate the notion that streams and riparian areas are difficult to manage because little is known about how these ecosystems function. Many agencies strive to develop procedures for treating the symptoms of degraded and potentially degraded ecosystems while giving little consideration to the causes. Other agencies and private interest groups showing con-

cern for conflicting issues like water allocations and minimum instream flows for fish commonly disagree with plans and recommendations for resolving these issues. The continuous dissent by these groups only adds to the plight of fish as available water, stream, and riparian resources continue to decline.

Historically, there are few management measures for effectively protecting and restoring these ecosystems. Some effective management actions for improving stream and riparian ecosystems include (a) moratoriums on riparian grazing; (b) road obliteration in riparian zones; (c) designation of riparian reserves prohibiting logging, road construction, and mining; (d) protection of unstable streambanks and adjacent hillslopes; (e) protection and restoration of refugia areas for fish and wildlife; and (f) reduction of sediment delivered to streams in both intact and damaged watersheds.

New basin-wide management strategies of federal agencies and environmental groups provide hope for improving the biodiversity and population levels of stream and riparian ecosystems (Doppelt *et al.* 1993, Forest Ecosystem Management Assessment Team 1993). Priorities include the protection, restoration, and monitoring of habitats and networks that connect stream and riparian ecosystems. The strategies emphasize ecosystem connectivity in both degraded and relatively intact watersheds. Intact and pristine watersheds (e.g., roadless and wilderness areas) serve to function as critical habitats and biotic refuge areas for fish and wildlife of adjoining ecosystems. The first priority is protection of critical habitats and networks connecting stream and riparian systems. This requires a basin-wide plan that considers the life history requirements of fish and wildlife using critical habitats.

Biotic refuges provide (a) sources of colonists to adjacent areas, (b) critical habitats for different life history stages, and (c) protective-cover and resting areas for migrating species (Sedell *et al.* 1990, Doppelt *et al.* 1993). Refuge areas of different river basins are identified by characteristics of natural habitat complexity, native species and high water quality. Refuge functions are provided by (a) intact headwater watersheds, (b) intact downstream river reaches and forested floodplains that contain internal interconnected refuges, and (c) small undisturbed but dispersed habitats like pools and side channels of stream ecosystems.

The second priority is the restoration of critical stream habitats and riparian corridors. The primary objective is to return stream and riparian structure, function, and ecosystem connectivity towards "natural conditions" that meet the life history requirements of fish and wildlife. A basin-wide strategy strives for securing and connecting refuge areas and critical habitats as well as providing connections to more degraded habitats. These restoration plans also provide for expanding floodplain areas to protect critical stream habitats and riparian corridors. An important criteria for success of restoration efforts is documentation of declines in interactions between human-induced impacts and natural disturbance regimes that create long-term cumulative effects.

The development of new management strategies for river basins east of the Cascade Mountains will require watershed screening analyses that use historic baseline data and field reconnaissances. These analyses serve to document functional and dysfunctional components of ecosystems. Large-scale, basin-wide assessments coupled to ongoing monitoring programs not only define ecosystem functions but help identify the most appropriate protection and restoration measures. Several federal agencies recommend watershed analyses for more detailed assessments of ecosystem functions (Forest Ecosystem Management Assessment Team 1993).

New generations of basin-wide management strategies (Doppelt *et al.* 1993, Forest Ecosystem Management Assessment Team 1993) will hopefully avoid the problems of past "band-aid management strategies." Band-aid strategies commonly identify the most degraded sites, allocate all funds to treat these areas, and then apply generic techniques to bring the sites "up to standards." These uncoordinated approaches do not identify and protect important refugia areas and ecosystem functions. Band-aid approaches usually cause refuge areas and critical habitats to be subject to continued disturbance and loss while the most severely damaged areas receive the restoration resources.

The implementation of basin-wide strategies for protection and restoration of streams and riparian ecosystems requires coordination between different management institutions. Coordination between resource managers, such as the Forest Service, Bureau of Land Management, Bonneville Power Administration, and state agencies in eastern Oregon and Washington can be accomplished by using

cooperative or joint monitoring programs. For example, when flood events in large river basins interact with dispersed landslides and road failures to form debris torrents, joint monitoring projects provide the capacity for evaluating basin-wide conditions related to streambank stability, responses of riparian vegetation, and changes induced in stream channels by sediment erosion and routing. Such monitoring programs need to be explicitly linked to specific objectives that include criteria for success (Wissmar 1993), for example, objectives that include criteria for assessing future conditions in restored ecosystems (Gore 1985, Maurizi and Poillon 1992).

The USDA Forest Service's management history favors the development of long-term monitoring programs for forest, stream, and riparian ecosystems in eastern Oregon and Washington. The Forest Service's history is the longest history of land-use planning of any government agency. The initial legal basis began with the Organic Act of 1897, which gave the Forest Service a wide management window to plan for improvement and protection of national forests for the purpose of "securing favorable conditions of water flow, and to furnish a continuous supply of timber."

A more recent act, the National Forest Management Act of 1976 (NFMA), sets a strong precedent for developing long-term strategies. NFMA focuses Forest Service management by requiring comprehensive Forest Plans. We recommend that the directives of the NFMA can be better implemented by developing cooperative basin-wide strategies and monitoring programs between agencies with objectives and activities rigorously attached to long-term time frames. Several publications provide useful information for developing new strategies for river basin management (National Research Council 1990, 1992a, b; the PACFISH strategy [USDA Forest Service 1992]; Forest Ecosystem Management Assessment Team 1993; Henjum *et al.* 1994). In closing, more historic perspectives of ecosystem protection and restoration do exist, as in Van Cleef's "How to restore our trout streams" (1885).

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Historical Changes in Fish Habitat for Select River Basins of Eastern Oregon and Washington

Abstract

From 1934 to 1942 the Bureau of Fisheries surveyed more than 8,000 km of streams in the Columbia River basin to determine the condition of fish habitat. Changes in fish habitat over time were evaluated by resurveying a subset of the historically surveyed streams in the Tucannon, Asotin, Grande Ronde, Yakima, Wenatchee, and Methow river basins from 1990 to 1992. Historical reviews show many streams as degraded from past land management practices (e.g., timber harvest, splash dams, stream channelization, livestock grazing, and mining) before the 1930s. Our basin resurveys show a decrease in large pools ($\geq 20\text{-m}^2$ area and $\geq 0.9\text{-m}$ depth) in managed watersheds (multiple-use, $p < .05$), while large pools in unmanaged watersheds remained the same or increased ($p < .05$). Results for these six river basins suggest a regional pattern to this change. Large pools increased in the Mid-Columbia region (Yakima, Wenatchee, and Methow basins; $p < .05$) regardless of management history, with the increase being twice as great in unmanaged watersheds. In the Blue Mountain region (Tucannon, Asotin, and Grande Ronde basins), large pools decreased significantly ($p < .05$). The current frequency of coarse woody debris was significantly higher ($p < .05$) in unmanaged than in managed basins. Differences in land-use histories for the mid-Columbia and Blue Mountain regions partially explain current fish habitat conditions and the declines in anadromous fish runs. Strategies to protect, restore, and maintain anadromous and resident fish habitat need ecosystem approaches that protect as well as restore the remaining habitats.

Introduction

In this paper we examine changes to fish habitat in selected river basins of eastern Oregon and Washington since the 1930s. The Pacific Northwest Research Station (PNW) has used Bureau of Fisheries (BOF, now National Marine Fisheries Service) fish habitat surveys conducted from 1934 to 1942, with current surveys, to detect changes in pool and substrate conditions over the past 60 years. To provide context and possible explanations for changes in fish habitat, we examined the land-use history of these basins. Additional historical information about the ecological health of river basins in eastern Oregon and Washington is given in Wissmar *et al.* (1994a,b).

Stream ecosystem integrity is coupled to the condition of upland areas and adjacent riparian areas (Gregory *et al.* 1991, Naiman *et al.* 1992). Riparian areas are sources of organic matter (e.g., coarse woody debris, litter), which forms the energy and nutrient base for many aquatic organisms. In addition, riparian areas strongly influence water temperature. Upland areas also provide coarse

woody debris (CWD) along with sediment, especially in small, permanently and seasonally flowing streams that may not hold fish. The creation and maintenance of productive aquatic ecosystems depends on maintaining the connectivity between stream, riparian, and upland areas. This connection is particularly strong in mountainous regions.

Pools and substrate composition are critical habitat components for anadromous salmonids (*Oncorhynchus* spp.) in all phases of their freshwater life histories. Pools provide rearing habitat for juvenile fish, resting habitat for adult fish (Bjornn and Reiser 1991), and refugia for adults and juveniles from natural disturbances, such as drought, fire, and winter icing (Sedell *et al.* 1990). Substrate composition affects the quality and quantity of spawning habitat, the availability of summer and winter cover for juvenile fish, and aquatic productivity (Bjornn and Reiser 1991). Salmonids are particularly sensitive to the effects of fine sediments ($< 6\text{ mm}$) in spawning gravels (Bjornn and Reiser 1991, Everest *et al.* 1987). A considerable body of literature has shown the detrimental effects of fine sediments on salmonid reproduction (Chapman 1988, Everest *et al.* 1987).

Decreased pool and substrate quality and quantity also affect aquatic biodiversity. The loss of fish habitat diversity caused by land-use practices alters fish community composition and reduces species diversity (Bisson *et al.* 1992, Bisson and Sedell 1984, Reeves *et al.* 1993). Research on Oregon

¹Department of Forest Science, Oregon State University, Corvallis, Oregon 97331

²Pacific Northwest Research Station, USDA Forest Service, 3200 SW Jefferson Way, Corvallis, Oregon 97331

³School of Fisheries, University of Washington, Seattle, Washington 98195

⁴Department of Fish and Wildlife, Oregon State University, Corvallis, Oregon 97331

coastal streams (Reeves *et al.* 1993) showed that species diversity in logged basins is lower than in similar, unharvested streams.

The scientific community agrees on the functional role of CWD in creating and maintaining high-quality fish habitat (Bisson *et al.* 1987, Hicks *et al.* 1991, Sedell *et al.* 1988). Coarse woody debris serves a wide array of physical and biological functions in stream ecosystems. In addition to cover and habitat complexity for fish, it also provides for sediment storage, channel roughness, reduced erosional effects of high flows, and enhanced pool development and maintenance. Several studies have shown that the loss of CWD causes reduced salmonid production (Bisson *et al.* 1987, Everest *et al.* 1985).

"Forest health," as it is generally perceived, is focused on the issue of dead and dying trees. To transcend this perception, managers and researchers must see the picture of forest health as one of watershed health, fully recognizing the intricate linkages between aquatic and terrestrial ecosystems. Stream ecosystems are the ultimate integrator of all watershed disturbances. If management plans aimed at restoring eastside forests fail to recognize and protect the critical linkages between terrestrial and aquatic ecosystems, the "health" of stream ecosystems and fish populations will continue to decline. Traditional approaches to stream restoration (i.e., in-stream structures) are at best band-aid measures with a high degree of uncertainty for success, especially in damaged systems (Beschta *et al.* 1991, Frissell and Nawa 1992, Li *et al.* 1992). Protecting aquatic ecosystems is by far the most efficient, cost-effective, and lowest-risk strategy to ensure long-term sustainability of these ecosystems (Reeves *et al.* 1991, Reeves and Sedell 1992). Management must center on a long-term, holistic approach that protects and maintains ecological processes at the scale of large watersheds (Naiman *et al.* 1992, Wissmar *et al.* 1994b).

Sedell and Everest (1990), McIntosh (1992) and McIntosh *et al.* (1994) have documented changes in the quality of fish habitat since 1934. The primary change has been the loss of large pools ($\geq 20\text{-m}^2$ area and $\geq 0.9\text{-m}$ depth) in watersheds managed for multiple use. These changes appear to be due to the effects of land-management activities, such as timber harvest, livestock grazing, agriculture, and mining. Multiple studies have documented the effects of land management activities on ecosystem processes and functions, such as increased sedimentation, mass

failures, and peak flows, as well as decreased CWD, bank stability, habitat complexity, and water quality (Meehan 1991).

Recent listing of chinook (*Oncorhynchus tshawytscha*) and sockeye salmon (*O. nerka*) in the Snake River basin under the Endangered Species Act (ESA) makes it imperative that a comprehensive, integrated approach to watershed health be initiated. In addition, the American Fisheries Society has documented 76 native anadromous salmonid stocks in the Columbia River basin that are at a high or moderate risk of extinction (Nehlsen *et al.* 1991). Over 200 stocks are already extinct in the Columbia River basin (Nehlsen *et al.* 1991). Status of resident fish, such as bull trout (*Salvelinus confluentus*), which are being considered for listing under ESA throughout their range in eastern Oregon and Washington, must also be fully considered.

Many factors have contributed to the demise of these fish species. They include habitat loss and degradation, influence of hatchery practices, over-exploitation in sport and commercial fisheries, and impediments to upstream and downstream movement by hydroelectric dams (Nehlsen *et al.* 1991, Northwest Power Planning Council 1986, Williams *et al.* 1989). These factors have not affected fish survival singularly, but cumulatively.

Increased survival in freshwater habitat, along with improved passage and reduced harvest, will be critical to the survival of these fish stocks. Fish habitats currently in good condition need protection and degraded habitats need restoration. Both protection and restoration are critical components of any ecosystem management plan developed to deal with forest health in river basins. Streams need less fine sediment, more shade, and increased habitat complexity to restore fish habitat to conditions that will support self-sustaining fish populations. Current strategies to protect and restore streams (Anderson *et al.* 1992, Hewjum *et al.* 1994, USDA 1993) call for enlarging riparian buffers, reducing road densities, and eliminating or reducing livestock grazing and any other activities detrimental to stream ecosystems.

Materials and Methods

Bureau of Fisheries stream surveys, together with resurveys, have been used by the PNW to detect changes in fish habitat in the Columbia River basin since 1934. We compared current surveys with the BOF surveys to detect changes in pool and substrate composition in the Blue Mountain and

Mid-Columbia regions. In addition, resurveys were used to evaluate current amounts of CWD in streams throughout the two regions.

From 1990 to the present, PNW examined streams across a broad range of geologic conditions, land ownerships, and land-use histories (McIntosh 1992, McIntosh *et al.* 1994, Sedell and Everest 1990). In conducting the resurveys, we attempted to examine streams across the Pacific Northwest to encompass as much variation as possible. This study does not account for the different potential of watersheds to create and maintain fish habitat because of differences in bedrock, soils, climate, stream discharge, vegetation, and structure. Ongoing research is being conducted in an attempt to analyze these results based on the inherent differences in watersheds.

Fish Habitat Surveys

The BOF surveys were initiated to determine the condition of streams in the Columbia River basin that provide potential spawning and rearing habitat for anadromous salmonids (Rich 1948). These records are the earliest and most comprehensive documentation of the condition and extent of anadromous fish habitat available. The BOF surveys systematically inventoried more than 8,000 km of streams in the Columbia River basin from 1934 to 1942.

Rich (1948) provided a detailed description of methods used in the BOF surveys. Data for the BOF surveys were systematically collected at continuous 100-yd intervals for the entire section surveyed, generally from the mouth to the upstream extent of anadromy. Within each 100-yd unit, the surveyors estimated channel width, estimated bottom substrate composition by size-classes and percentage per class, and counted the number of pools by size-class.

Historically surveyed streams were resurveyed by using the Hankin-Reeves method (Hankin and Reeves 1988). This sampling technique involves stratifying streams according to channel units (e.g., pool, riffle, glide). Channel units for the resurvey were based on morphological characteristics rather than on an arbitrary length, as were the BOF surveys. The Hankin-Reeves method provides data that are comparable with the BOF surveys.

To examine changes in fish habitat over time, we classified individual streams according to the land-management history of the basin. Basins were

classified as either managed or unmanaged. Managed basins were predominantly multiple-use areas (e.g., for timber, livestock, agriculture, and mining production). Unmanaged basins were minimally affected by human disturbance (i.e., wilderness and roadless areas). We recognize that many unmanaged basins were affected by grazing and mining historically. In the absence of suitable data, we surmise that grazing use has declined in unmanaged basins similar to managed basins.

Pool Habitat

Analysis of changes in pool habitat was based on large pools ($\geq 20\text{-m}^2$ area and $\geq 0.9\text{-m}$ depth). To account for hydrologic variability and provide a conservative estimate of changes in pool frequencies, we effected an intentional bias by discarding marginal pools from the BOF surveys and including marginal pools in the resurveys. In the BOF surveys, marginal pools were those noted as shallow or small and were not included in the analysis. Marginal pools added to the 1990 total were large pools ($\geq 0.8\text{ m}$ depth). In effect, the data represent two biases: a bias for fewer pools historically and a bias toward more pools in the resurveys. A two-sample *t*-test was used to compare pool frequencies between the BOF surveys and the resurveys.

Substrate Composition

To assess changes in substrate, we compared mean substrate composition, dominant substrate, and fine sediments between the two surveys. One significant failure of both surveys is the lack of an error term for estimates of substrate composition. Both the BOF and current estimates were not corrected for observer bias, eliminating any means of quantifying the variability associated with the estimates. This limits the usefulness of the data to determining trends in substrate conditions.

Coarse Woody Debris

In the resurveys data were collected on the quantity of CWD in channels. The BOF survey did not collect data on CWD. We counted the number of pieces and noted the positions of CWD as single pieces or in jams ($\geq$ two pieces). The minimum size for CWD was $\geq 0.1\text{-m}$ diameter and $\geq 2.0\text{-m}$ length. A two-sample *t*-test was used to compare the frequency of CWD in managed and unmanaged basins.

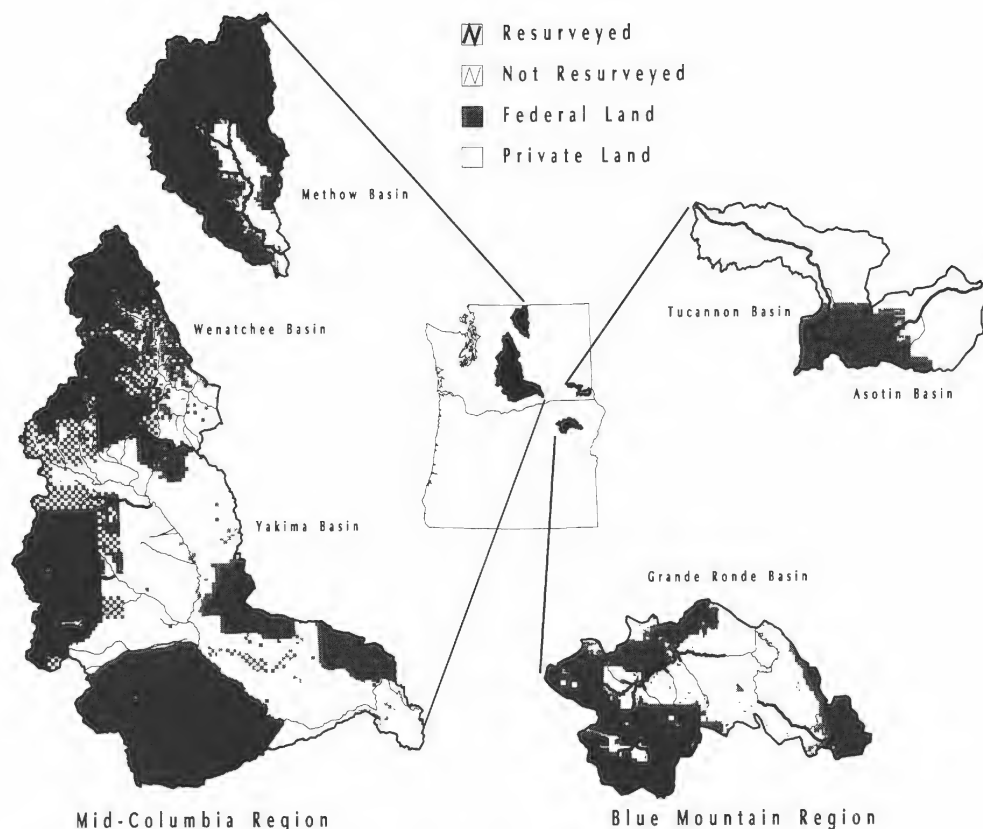


Figure 1. Map of study basins and surveyed streams in eastern Oregon and Washington.

Land-Use History

The available records of land-use history for the study basins, along with more general regional records, were examined to characterize the land management history before and after the BOF surveys. The disturbance history provides the context for identifying potential causal mechanisms for changes in fish habitat. The information complements the land-use and disturbance history available from both public and private sources (Wissmar *et al.* 1994b).

Study Area

In this study, we examined river basins in eastern Oregon and Washington where resurveys were conducted between 1990 to 1992. These resurveys included portions of the Tucannon, Asotin, Grande

Ronde, Yakima, Wenatchee, and Methow river basins. We separated these river basins into two regions for further comparison. The Blue Mountain region consisted of the Tucannon, Asotin, and Grande Ronde basins, and the Mid-Columbia region contained the Yakima, Wenatchee, and Methow basins (Figure 1).

Blue Mountains Region

Tucannon River basin. The Tucannon River basin, in southeast Washington, drains an area of 1,300 km². The BOF surveyed the Tucannon River and its major tributaries in 1935; the resurveys were limited to the Tucannon River. More than 70% of the basin is private land, and the remainder is public land. Headwater portions of the basin are wilderness areas, and the forested reaches below the wilderness are managed for multiple use by

the Forest Service. From the Forest Service boundary to the mouth, the remainder of the basin is private land. Private lands are managed predominantly as dry croplands and rangelands (USDA Soil Conservation Service 1991).

The basin supports summer steelhead (*O. mykiss*) and spring chinook; spring chinook is listed as threatened under the ESA, and summer steelhead is listed as a species of special concern by Nehlsen *et al.* (1991). Historically the Tucannon supported coho salmon (*O. kisutch*), which is now extinct in the basin. Bull trout is also found in the upper portions of the basin.

Asotin Creek basin. Asotin Creek is in southeast Washington, draining an area of 828 km². The upper mountainous, forested portions of the basin are managed for multiple use by the Forest Service. Lower portions of the basin are private and are used for dryland crops and rangeland (USDA Soil Conservation Service 1991).

The Asotin basin supports spring chinook and summer steelhead. Spring chinook is listed as threatened under the ESA, and Nehlsen *et al.* (1991) list summer steelhead at a moderate risk of extinction. Current populations of anadromous fish in the Asotin basin are far below historical levels.

Grande Ronde River basin. The Grande Ronde River basin, in northeast Oregon, encompasses ~12,810 km². The BOF surveys were limited to the upper portion of the basin, from the Grande Ronde valley to the headwaters. About 50% of the Upper Grande Ronde River basin is public land managed by the Forest Service; most of the land is mountainous and timbered. The valley bottoms are predominantly privately owned, and the primary uses are livestock grazing and agriculture (McIntosh 1992, Northwest Power Planning Council 1990).

Historically, the Upper Grande Ronde River basin had large runs of anadromous salmonids. The basin supported spring chinook, coho, and summer steelhead (Northwest Power Planning Council 1990). These runs have been reduced to a small fraction of their pre-development numbers, with coho being extinct in the Grande Ronde and spring chinook listed as threatened under the ESA.

Mid-Columbia Region

Yakima River basin. The Yakima River basin, in south-central Washington, drains an area of

15,942 km². More than 60% of the land in the Yakima basin is publicly owned, and the remainder is in private ownership. Irrigated agriculture is the current economic base, with livestock production and forestry also contributing to local economies (Northwest Power Planning Council 1989).

Historically, the basin supported summer steelhead, coho, chinook, and sockeye salmon. Pre-development run sizes (pre-1870) were estimated at 790,000 adults (Northwest Power Planning Council 1989, Table 1). By the turn of the century, most runs were depleted, with coho and sockeye near extinction (Uebelacker 1980). Currently, coho, summer chinook, and sockeye salmon are extinct in the basin, and summer steelhead, fall, and spring chinook are listed as stable (The Wilderness Society 1993).

Wenatchee River basin. The Wenatchee River basin is in north-central Washington; it drains an area of 3,437 km². The basin is about 80% public land, mostly in the mountainous, forested regions. Irrigated agriculture, along with livestock and forestry, is the current economic base.

Historically, the Wenatchee had large runs of steelhead, chinook, and sockeye salmon, as well as a small coho salmon run. Coho were extinct in the basin by the 1940s. Recent research (Mullan *et al.* 1992) suggests that current wild run sizes appear to be similar to historical populations (Table 1). Although the current population seems stable, the species composition of the run has shifted significantly. Chinook salmon comprise most of the run; sockeye salmon populations are reduced and coho salmon are extinct in the basin. Summer steelhead is listed as a species of special concern by Nehlsen *et al.* (1991) primarily because of the effects of hatchery introgression.

Methow River basin. The Methow River basin is in north-central Washington; it drains an area of 4662 km². About 80% of the basin is public land managed by the Forest Service, predominantly in the upper portions of the basin. The lower portions are privately owned. Logging and livestock production is the economic base of this sparsely populated basin, with fruit orchards also playing a significant role (Mullan *et al.* 1992).

Before settlement by Euro-Americans, the Methow supported significant runs of chinook and coho salmon, along with steelhead, with coho being the most abundant (Mullan *et al.* 1992, Table 1). Currently, chinook salmon and steelhead

TABLE 1. Estimates of historical salmon and steelhead runs in the Yakima, Wenatchee, and Methow River basins (Northwest Power Planning Council 1989, Mullan *et al.* 1992).

Species/race	Run size	
	Historical	Present
Yakima River Basin	790,000	7,018 ^a
Wenatchee River Basin	280,600	306,700 ^b
Methow River Basin	63,800	91,100 ^c

^aBased on mean run size for all anadromous salmonids from 1983 to 1987.

^bBased on mean run size for all anadromous salmonids from 1967 to 1987.

^cBased on mean run size for all anadromous salmonids from 1967 to 1987.

remain, and coho salmon are extinct in the basin. Mullan *et al.* (1992) suggest that current runs exceed the historical runs in the Methow basin, with chinook replacing coho (Mullan *et al.* 1992). Wild steelhead is listed at a high risk of extinction by Nehlsen *et al.* (1991) primarily because of the impacts of irrigation and hatchery introgression.

Results

Changes in fish habitat in eastern Oregon and Washington (Table 2) were similar to the results for the Columbia River basin (Table 3). The trend

towards decreased pool frequencies in managed watersheds was not significant ($p > .05$) but showed a regional pattern. Pool frequencies in unmanaged watersheds increased significantly (2.0-5.9 pools/km, $p < .05$) (Table 2). Trends in substrate composition were variable. The survey results indicated that the frequency of CWD was significantly greater ($p < .05$) in unmanaged watersheds (Table 4). In the following sections, we examine the changes in individual river basins to further illustrate these changes.

Blue Mountain Region

The PNW, in cooperation with Oregon State University, resurveyed 260 km of streams in the Blue Mountain region from 1990 to 1992 in the Tucannon, Asotin, and Grande Ronde basins. The surveyed streams went from headwaters to low-gradient, alluvial rivers, across both public and private lands. None of the streams surveyed in the Blue Mountain region could be classified as unmanaged, leaving no minimally disturbed benchmark against which to evaluate change.

Pool Habitat

Resurveys in the Blue Mountain region show that the frequency of pools decreased by 57% (mean = 5.6 to 2.4 pools/km, $p < .05$, Table 5) in managed watersheds. The Tucannon River was the

TABLE 2. Changes in the frequency of large pools for streams in managed and unmanaged watersheds of selected river basins in eastern Washington and Oregon from 1934 to 1992.

	Km surveyed	1934-42 #/km	1990-92 #/km	Percentage change
<i>Managed</i>				
Tucannon River, WA	64.5	2.4	6.5	171%
Yakima River, WA	65.4	1.8	3.8	111%
Methow River, WA	146.0	1.7	3.4	100%
Wenatchee River, WA	33.6	4.9	7.7	57%
Asotin Creek, WA	37.5	3.1	2.1	-33%
Grande Ronde River, OR	157.9	6.1	2.1	-66%
Total (n = 21)	505.0	4.3	3.1	-28%
<i>Unmanaged</i>				
Methow River, WA	30.2	1.0	3.4	240%
Wenatchee River, WA	80.2	2.5	7.5	200%
Yakima River, WA	18.8	1.6	3.9	144%
Total (n=5)	129.2	2.0	5.9	195% ^a

^aDifferences between the BOF surveys and current surveys significant at $p < .05$

TABLE 3. Changes in the frequency of large pools for streams in select managed and unmanaged basins in the Columbia River Basin from 1934 to 1992.

	Km surveyed	1934-42 #/km	1990-92 #/km	Percentage change
Managed basins	1411.0	7.5	5.4	-28% ^a
Unmanaged basins	265.0	3.9	6.9	77% ^a

^aDifferences between the BOF and current surveys significant at $p < .05$

TABLE 4. Current frequency of coarse woody debris (≥ 0.1 -m diameter and ≥ 2.0 -m length) for streams in selected managed and unmanaged watersheds of eastern Oregon and Washington.

	Coarse woody debris	
	Pieces (#/km)	Jams (#/km)
<i>Managed</i>		
Grande Ronde basin, OR	36.0	5.9
Yakima River basin, WA	32.8	5.8
Wenatchee River basin, WA	26.7	3.5
Methow River basin, WA	69.2	12.3
	MEAN 41.8	7.1
<i>Unmanaged</i>		
Yakima River basin, WA	72.7	13.8
Wenatchee River basin, WA	72.5	11.9
Methow River basin, WA	40.2	8.1
	MEAN 66.1 ^a	11.5 ^a

^aDifferences between managed and unmanaged basins significant at $p < .05$.

only stream that showed an increase in pool frequencies (2.4 to 6.5 pools/km). There were no unmanaged watersheds for comparison in this region.

Our most extensive overview of changes in fish habitat was from the Grande Ronde basin (McIntosh 1992); surveys in the Tucannon and Asotin basins were limited to the Tucannon River and Asotin Creek. The BOF surveys in the Grande Ronde were in the upper basin, from the Grande Ronde valley to the headwaters. In 1990 all historically surveyed streams in the Upper Grande Ronde River basin were resurveyed (McIntosh 1992). These streams extend across a variety of landscapes (e.g., mountainous, meadow), land-use histories (e.g., logging, mining, agriculture) and land ownerships (i.e., public, private).

Survey results indicate that pool habitat decreased significantly ($p < .05$) throughout the

Grande Ronde basin despite differences between streams. The frequency of large pools in the BOF surveys ranged from 0.0 to 14.6/km (mean = 6.1/km, Table 2). In 1990 pool frequencies ranged from 0.0 to 7.0/km (mean = 2.1/km, Table 2). The loss in large pools ranged from 20% to 87%, with a mean of 66% (Table 5). In the BOF surveys pool frequencies were highly variable ($VAR = 23.2$) among the different streams, but the 1990 survey showed that pool frequencies were similar ($VAR = 3.2$) for all streams. The decreased variability in pool frequencies showed that habitat diversity decreased significantly.

Substrate Composition

Trends in substrate composition varied among the three basins. No change was found in substrate composition for Asotin Creek, but the Tucannon

TABLE 5. Changes in the frequency of large pools for selected streams in managed watersheds of the Blue Mountain region from 1934 to 1992.

	Km surveyed	1934-42 #/km	1990-92 #/km	Percentage change
Tucannon River basin				
Tucannon River	64.5	2.4	6.5	171%
Asotin Creek basin				
Asotin Creek	37.5	3.1	2.1	-33%
Grande Ronde basin				
Rock Creek	2.2	0.0	0.9	90%
Jordan Creek	3.1	0.0	0.0	NC
Five Points Creek	2.8	1.8	1.8	NC
Meadow Creek	18.6	2.5	2.0	-20%
Sheep Creek	9.2	14.6	6.8	-53%
Catherine Creek	30.7	9.2	3.6	-61%
N Fk Catherine Creek	6.6	4.7	1.7	-64%
Grande Ronde River	73.4	4.0	1.1	-73%
McCoy Creek	4.7	9.1	1.7	-81%
Beaver Creek	3.3	10.0	1.5	-85%
S Fk Catherine Creek	3.3	11.2	1.5	-87%
TOTAL	259.9	5.6	2.4	-57% ^a

^aDifferences between the BOF surveys and current surveys significant at $p < .05$

River showed a shift toward larger substrates. Fine sediments remained at low levels in Asotin Creek (6%) and the Tucannon River (7%). Substrate composition in the Upper Grande Ronde River basin shifted toward finer substrates. Substrate composition changes throughout the basin, with finer sediments being deposited downstream in the Grande Ronde River.

Analysis of mean substrate composition suggested no change in fine sediments in the Upper Grande Ronde River basin although fine sediments were 20% of the substrate composition in the Grande Ronde River. The spatial distribution of fine sediments relative to anadromous salmonid habitat was examined by plotting the percentage of surface fines for individual channel units from the downstream to upstream extent of the Upper Grande Ronde River. This spatial analysis showed that fine sediment in the headwater portions of the Upper Grande Ronde River greatly exceeded 20% of the substrate composition throughout most of this reach (McIntosh 1992). In addition, most of the stream channels throughout the headwaters are highly embedded, generally exceeding current standards of 35% (USDA Forest Service 1991, 1992a).

Land-Use History

Our survey of land-use history was limited to the upper Grande Ronde basin. Future work will examine the Tucannon and Asotin basins in greater detail. The history of Euro-American development and land use in the Grande Ronde basin may be indicative of the general pattern for the Blue Mountain region of northeast Oregon and southeast Washington. Wissmar *et al.* (1994b) detail the land-use history of the John Day basin, showing its similarity to the Grande Ronde basin.

At the time of the BOF surveys, the Upper Grande Ronde River basin had already experienced considerable human-induced disturbance. Available records of land-use history for this basin were examined to characterize land-use history before and after the BOF surveys. Records of timber harvest, road construction, and livestock grazing were available from the Wallowa-Whitman National Forest.

Mining. Mining was the first influence of Euro-Americans in the Upper Grande Ronde River basin. The headwaters of the basin have been mined for gold since 1870, with extensive dredge mining in the early 1900s. Gold mining has

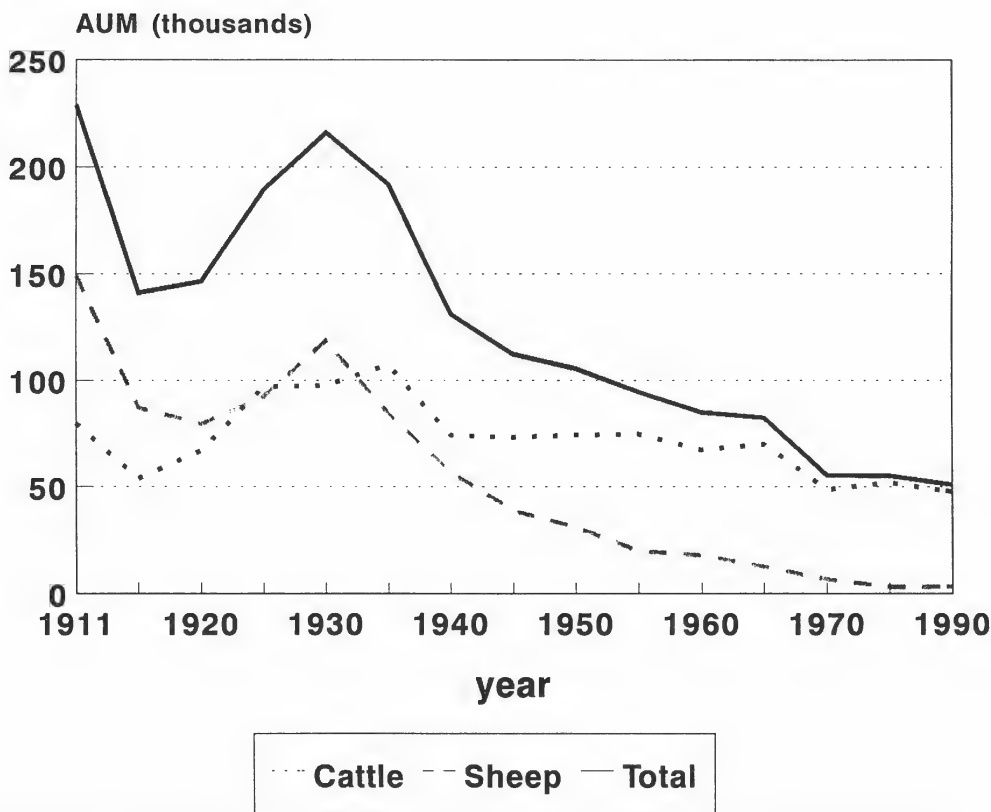


Figure 2. Grazing use (animal unit month) for livestock and elk on the Wallowa-Whitman National Forest, 1911 to 1990.

significantly altered the river and its floodplain throughout the headwaters. Extensive mine tailings from dredging throughout the upper river constrict the mainstem channel and provide a continuous source of sediment. This reach of the river currently provides most of the spring chinook spawning habitat in the Upper Grande Ronde.

Livestock grazing. Early records of livestock grazing in the Upper Grande Ronde basin suggest that parts of the basin were overgrazed by the 1880s (Skovlin 1991). Records of annual grazing use were available from the Wallowa-Whitman National Forest from 1911 to 1990. Over that period, grazing by livestock (cattle and sheep) declined 78% (Figure 2). The decline in grazing was largely due to the collapse of the sheep industry in northeast Oregon. Cattle represent > 90% of the grazing animals today.

Timber harvest. The historical record of timber harvest in the Upper Grande Ronde River basin shows that logging began in the late 1800s (Farnell 1979). Harvest has increased steadily since 1896, with the most intensive logging coming after 1950 (Figure 3), primarily in response to insect outbreaks (Wickman 1991).

Although harvest has increased over time, the effects of spatial patterns of harvest and harvest methods must also be considered. Harvest in the early part of the century was restricted to riparian areas and the adjacent hillslopes, and primarily selected for mature ponderosa pine (*Pinus ponderosa*). Logs were moved to the mills first by log drives and splash dams (1890-1919), then by rail (1910-1954), and finally by roads (1930-present).

In the latter part of the century, higher elevation and headwater sections of the basin were

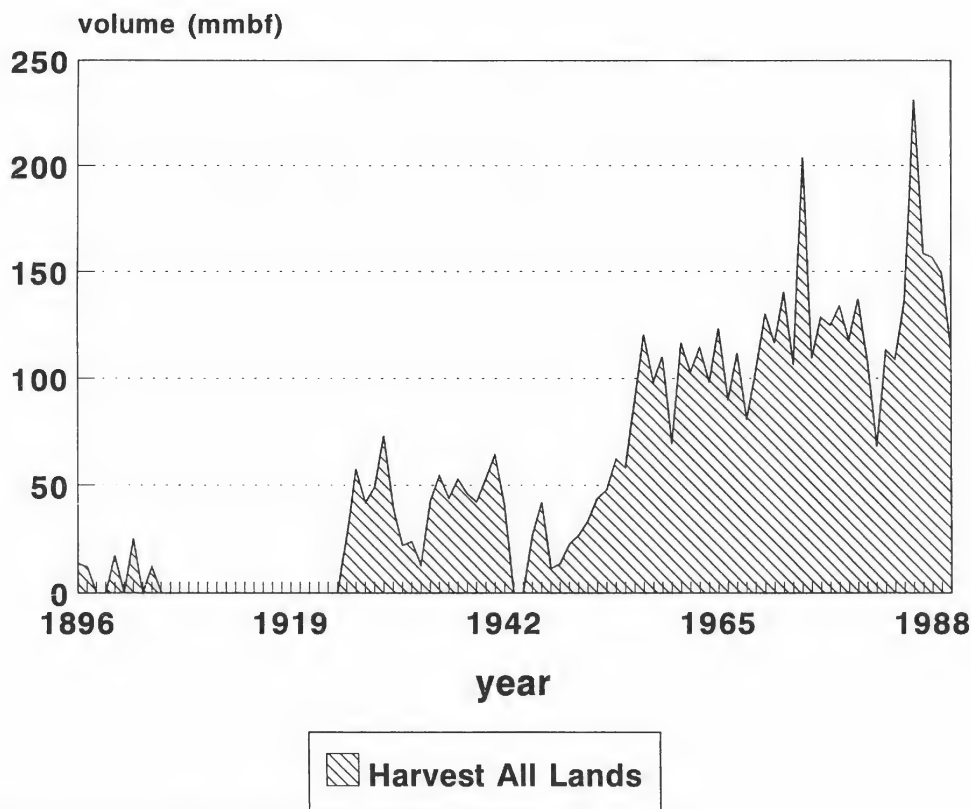


Figure 3. Volume of timber harvested (mmbf) for Union County, Oregon, 1896 to 1990.

accessed as road construction increased. From 1954 to 1978, road mileages increased more than twofold (3,200-7,200 km), doubling again from 1978 to 1989 (7,200-16,000 km, Figure 4). Clear-cutting and selective harvest became the preferred methods of harvest from the 1950s to the present.

Stream channelization. The influences of stream channelization appear in the Upper Grande Ronde basin. Stream channelization projects attempted to protect private property from flooding by "locking" the stream channel in place with riprap and levees. The periods of most intensive activity were often in response to major floods, such as the 1964 flood.

Mid-Columbia Region

From 1990 to 1992, the PNW, in cooperation with the University of Washington and the Wenatchee

and Okanogan National Forests resurveyed over 370 km of historically surveyed streams in the Yakima, Wenatchee, and Methow River basins. The surveyed streams range from small, mountainous streams to large, alluvial rivers. These streams extend across both private and public land and have various land-use histories. Although these surveys represent a small sample of BOF streams in these basins, we believe they represent the types of change that streams in this region have undergone since Euro-American settlement.

Pool Habitat

Survey results show that large pool habitats increased significantly ($p < .05$) in both managed and unmanaged watersheds in the Yakima, Wenatchee, and Methow River basins since 1934 (Table 6). Of the 11 streams we surveyed, only

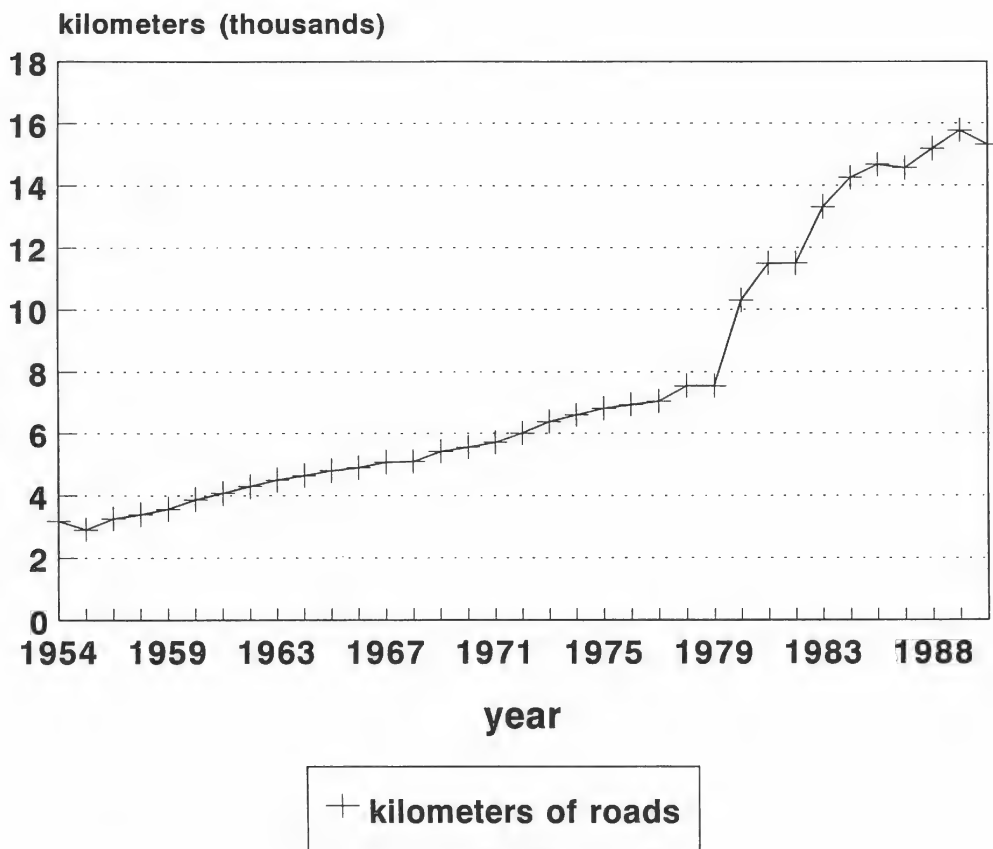


Figure 4. Road mileage (km) on the Wallowa-Whitman National Forest, 1954 to 1990.

the American River had a decrease (3.3-2.4 pools/km) in pool habitat. Pool frequencies were similar for both managed (mean = 2.2 pools/km) and unmanaged watersheds (mean = 2.0 pools/km) in the BOF surveys. In the resurveys, the increase in pool habitat was twice as great in unmanaged watersheds (2.0-5.9 pools/km) as in managed watersheds (2.2-4.1 pools/km).

Pool habitats increased by a similar magnitude in both managed (1.8-3.8/km, 111%) and unmanaged (1.6-3.9/km, 144%) portions of the Yakima basin. In the Wenatchee and Methow basins, a twofold to threefold greater increase in pool frequencies was found in unmanaged versus managed watersheds.

Substrate Composition

The resurveys indicated that changes in substrate composition were highly variable. Substrate composition appeared to change little in unmanaged watersheds; changes in dominant substrate were common in managed watersheds. In the Yakima basin, substrate composition shifted toward larger substrates in the Little Naches River and Taneum Creek (Smith 1993), but it remained the same in Rattlesnake Creek. No substrate data were available for the American River. Fine sediments increased in Taneum Creek (7-18%). Increased fine sediment, along with high levels of embeddedness, suggested that fine sediments have increased since 1934 (Smith 1993).

TABLE 6. Changes in the frequency of large pools for streams in selected managed and unmanaged watersheds in the Mid-Columbia region from 1934 to 1992.

	Km surveyed	1934-42 #/km	1990-92 #/km	Percentage change
<i>Managed</i>				
Yakima River basin				
Taneum Creek	17.3	0.5	3.4	580%
Little Naches River	15.6	1.7	4.6	171%
Rattlesnake Creek	8.0	1.9	4.6	142%
American River	24.5	3.3	2.4	-27%
Wenatchee River basin				
Nason Creek	33.6	4.9	7.7	57%
Methow River basin				
Chewack River	33.9	1.0	3.5	250%
Methow River	69.7	1.4	3.0	114%
Twisp River	42.5	2.8	3.9	37%
TOTAL	245.1	2.2	4.1	86% ^a
<i>Unmanaged</i>				
Yakima River basin				
Rattlesnake Creek	18.8	1.6	3.9	144%
Wenatchee River basin				
Jack Creek	6.9	1.9	8.0	321%
Iceicle Creek	14.2	3.7	10.2	171%
Chiwawa River	59.1	1.8	4.2	133%
Methow River basin				
Chewack River	30.2	1.0	3.4	240%
TOTAL	129.2	2.0	5.9	195% ^a

^aDifferences between the BOF surveys and the current surveys significant at $p < .05$.

Changes in dominant substrate were also variable for surveyed streams in the Wenatchee River basin. Of the unmanaged streams, Jack Creek and the Chiwawa River remained the same, but Iceicle Creek shifted to smaller substrate classes. Nason Creek, the managed stream, also shifted toward smaller substrates.

Comparisons of substrate composition of the streams in the Methow River basin suggested no significant trends. The exception was the Methow River, where the dominant substrate shifted to smaller substrates.

Land-Use History

The early Euro-American development of the Mid-Columbia region followed a similar pattern to that of the Blue Mountain region. After the 1930s, development in the Mid-Columbia region was different from the Blue Mountain region. Mining was one

of the first activities during the settlement era, beginning in the 1850s (Wissmar *et al.* 1994b). The floodplain and streambeds have been affected more extensively by mining for nonmetallic resources (e.g., gravel, sand, limestone) (Wissmar *et al.* 1994b).

Livestock grazing. Livestock grazing began in the 1850s; cattle populations peaked in the 1880s and sheep populations peaked at the turn of the century and again during World War I (Smith 1993). Before 1890 effects of grazing were concentrated in the lower portions of the basin. As grazing pressures increased, use expanded to all portions of the basins. Cattle and sheep used the high meadows for summer range, moving to the valley bottoms for winter. By 1907, public outcry over overgrazing was heard in the Yakima basin (Cooperative Western Range Study 1938). In the 1930s livestock populations declined from historical peaks and

allotment management systems replaced the open range (S. Carter, Supervisor's Office, Wenatchee National Forest, Wenatchee, WA, unpubl. data).

Timber harvest. The earliest records of timber harvest show logging began in the late 1800s in the Mid-Columbia region (Plummer 1902). Until the 1950s, timber harvest was largely limited to selective logging of mature conifers from the valley bottoms and adjacent hillslopes (Smith 1993), with little harvest on public lands until the 1960s. From the mid-1970s to the present, clearcutting became a common practice, and the volume of timber harvested increased significantly. Accompanying these practices was a substantial increase in road construction.

The highest timber harvests for the Mid-Columbia region were recorded in the 1980s (Mullan *et al.* 1992). Even with increased harvest in the past decade, 65% of the Wenatchee and 75% of the Okanogan national forests, remain in wilderness or roadless designation (USDA Forest Service 1989, 1990). Timber harvest in this region has not been either as intensive or extensive as that documented for the Blue Mountain region.

Irrigation and dams. Irrigated croplands are the dominant form of agriculture in the Mid-Columbia region (Mullan *et al.* 1992). Extensive fruit orchards and croplands are present in all the major river valleys, providing the primary economic base for the region (Northwest Power Planning Council 1989). The major effects early in the century were from dams and irrigation diversions with inadequate bypass or screening facilities. For example, a hydroelectric dam near the mouth of the Methow River completely blocked the upstream migration of anadromous salmonids from 1912 to the 1930s. This barrier caused the extinction of coho salmon in the basin and severely reduced other anadromous runs (Mullan *et al.* 1992, Wissmar *et al.* 1994b). Currently, inadequate screening and variable streamflows remain a problem in many areas. For a more thorough review of the effects of irrigation and dams, see Wissmar *et al.* (1994b).

Coarse Woody Debris

Resurveys showed that the frequency of CWD was significantly higher ($p < .05$) in unmanaged than in managed basins of eastern Oregon and Washington (Table 4). The frequency of CWD pieces and jams was 58% and 62% greater in unmanaged basins than in managed basins. The exception was

the Methow basin, where the frequency of CWD was greater in managed than in unmanaged watersheds.

Data on current frequencies of CWD in the Blue Mountain region were limited to surveys in the Grande Ronde basin. Current Forest Service surveys show that streams in managed watersheds throughout the upper Grande Ronde basin have a low frequency of CWD, while unmanaged portions have higher frequencies (USDA Forest Service 1991, 1992a). The frequency of CWD in the upper Grande Ronde was similar to other managed river basins surveyed in eastern Oregon and Washington, but far less than in unmanaged basins.

Discussion

This historical study shows that fish habitat has changed in selected river basins of eastern Oregon and Washington since 1934. Pool habitat decreased significantly in the Blue Mountain region and increased in the Mid-Columbia region. Substrate conditions shifted toward smaller substrates in managed watersheds and remain unchanged in unmanaged watersheds. Fine sediments also increased in some basins, especially the Grande Ronde. Current frequencies of CWD are much higher in unmanaged than in managed watersheds.

The changes in pool habitat are distinct for the two regions. Pool habitat increased in the Mid-Columbia region whether the watershed is managed or unmanaged, although the increase is twice as great in unmanaged watersheds. In the Blue Mountain region, the loss in pool habitat is large and consistent. The exception is the Tucannon River, where pool habitat increased significantly. Our field observations suggest that recovering riparian vegetation and reduced sedimentation contribute to improved conditions in the Tucannon. The headwaters of the Tucannon are largely intact because of wilderness protection. Although the trend toward improved fish habitat is positive, the Tucannon and Grande Ronde basin water temperatures are at sublethal to lethal for salmonids throughout much of the summer (Theurer *et al.* 1985, Bohle 1994).

Shifts in substrate composition for streams in managed watersheds suggested altered sediment supplies. Changes in substrate size can signify impacts of sediment inputs (Dietrich *et al.* 1989) and

bedload transport in the stream (Heede 1980). Given current and past management practices, both have likely occurred (Dunne and Leopold 1978, Richards 1982). These changes can result in channel-widening, leading to increased water temperatures (MacDonald *et al.* 1991), decreased pool volumes (Lisle and Hilton 1992), and changes in species composition (Reeves *et al.* 1993). Increases in fine sediments can significantly lower egg survival (Bjornn and Reiser 1991, Everest *et al.* 1987) and decrease or eliminate pool habitat (Lisle and Hilton 1992).

Significantly lower amounts of CWD in managed watersheds, coupled with the history of CWD removal, show the extent to which the functional role of CWD decreased in the managed systems. The loss of CWD reduces habitat complexity, channel roughness, and sediment storage, and may contribute to lower salmonid survival (Bisson *et al.* 1987). These decreases in CWD in managed systems appear to be due to the effects of past land management practices, such as splash dams, debris-removal programs, and riparian timber harvest (Sedell *et al.* 1991). These practices may also influence future recruitment of CWD in managed stream ecosystems. Analysis of current forest practices rules in Oregon and Washington suggests that the recruitment of CWD will decrease with each succeeding harvest rotation (Heimann 1988, Oregon Department of Forestry 1992).

The status and trends in pool habitat, substrate conditions, and CWD indicate that streams in managed watersheds are simplified compared with those in unmanaged watersheds. Managed streams show decreased frequencies and diversities of habitat types (i.e., pools, riffles, side-channels), CWD, and other structural elements common to unmanaged streams (Reeves and Sedell 1992). This study suggests the general trend for the entire Columbia River basin is toward a loss in pool habitat on managed lands and stable or improving conditions on unmanaged lands. Water quality (i.e., temperature, turbidity) may also be reduced in many of the managed streams.

Fish habitat conditions in river basins surveyed in the Mid-Columbia region appear to be recovering to some extent from past land management practices. In contrast, fish habitat conditions in the Blue Mountain region declined significantly over the past 5 decades. A possible explanation is the differing land management history documented for the two regions. Minimal human disturbance af-

fected the surveyed portions of the Mid-Columbia region from the 1930s to the 1970s, while the opposite occurred in the river basins of the Blue Mountain region. The cumulative effects of land management practices have exacerbated or magnified the effects of any one factor operating in isolation.

The historical records show that during early Euro-American settlement (1850 to 1930), these two regions experienced similar land-use histories. During this period the major influence on stream ecosystems is attributed to livestock grazing. Sheep grazed the high meadows while cattle grazed the floodplains in numbers that far exceeded the capacity of the range (Platts 1991, US EPA 1990). Anecdotal reports and photographs depict summer ranges so heavily stocked with sheep, they look like snow drifts. The legacy of this period is still evident throughout the eastern Oregon and Washington as witnessed by the terraced hillslopes caused by the constant trodding of millions of hoofs through the decades.

Although livestock use has declined since the 1930s, concern for aquatic ecosystems increased with the shift from sheep to cattle. In general, cattle can have a greater effect on streamside areas than sheep (Platts 1991, Wissmar *et al.* 1994b). Although improved rangeland conditions tended to occur in the upland areas, little improvement was noted in riparian areas. For a more detailed discussion on range conditions and the influences of grazing on riparian ecosystems see Platts (1991) and Wissmar *et al.* (1994b).

With the decline of the livestock industry in the 1930s, the similarity in land-use histories for the two regions ended. The Blue Mountain region was along the main migration route to the Pacific Northwest (e.g., Oregon Trail), which caused this area of Oregon to be developed more rapidly. The Mid-Columbia region was relatively isolated. As the livestock industry throughout eastern Oregon and Washington declined, the timber industry began to expand in eastern Oregon. Demand for timber was the result of expanding railroads and growing populations. The timber industry boomed after World War II, steadily increasing to the present. Local economies in eastern Oregon have been dominated by timber since.

Recent research (Mullan *et al.* 1992, Wissmar *et al.* 1994b) suggests that the land-use history in the Mid-Columbia region differed from that west

of the Cascades and in the Blue Mountain region, where land-use patterns appeared to have different influences on riverine ecosystems. As livestock grazing declined, development pressures were concentrated in the larger river valleys (e.g., Yakima and Wenatchee), where irrigated agriculture became the economic base. Headwater and tributary portions of the basins were minimally affected. This pattern corresponds with land allocations on the Wenatchee and Okanogan national forests; more than 65% of their land base occurs in wilderness or roadless areas. Human activities increased in the upper portions of the basins as timber harvest and road construction began in the late 1950s. These activities shifted over time from selective harvest to clearcutting. Since the 1970s, timber harvest increased throughout the Mid-Columbia region (Wissmar *et al.* 1994b).

The period of reduced human development (1930-1970s) in the tributary portions of Mid-Columbia basins, followed by much later entry for timber harvest, may explain the trend toward increased pool habitat. Pool frequencies were the same for managed (2.2 pools/km) and unmanaged (2.0 pools/km) watersheds in the BOF surveys. In the current surveys, the increases were twice as great in the unmanaged (5.9 pools/km) than in managed (4.1 pools/km) watersheds. The data suggest that unmanaged systems may be more structurally intact (i.e., CWD, habitat diversity, riparian vegetation), allowing a positive interaction with the stream processes (i.e., peak flows, sediment routing) that shape and maintain high-quality fish habitat over time.

Although the trends toward increased pool habitat in the Mid-Columbia region are encouraging, poor fish habitat conditions remain in many managed watersheds. High water temperatures, inadequate stream flows, and high levels of fine sediments have been documented in many managed watersheds, especially in the Yakima basin (Fast *et al.* 1991, Northwest Power Planning Council 1989, Smith 1993). Given the late entry for timber harvest, fish habitats may not be expressing the cumulative effects of harvest activities of the past 20 yrs. Protecting stream ecosystems should be a management priority to continue these improving trends.

Our data suggest that fish habitats are in better condition in the Mid-Columbia than in the Blue Mountain region. This conclusion is further strengthened by the stable condition of most

anadromous runs in the Mid-Columbia region (Mullan *et al.* 1992, Nehlsen *et al.* 1991, The Wilderness Society 1993). In contrast, most anadromous runs in the Blue Mountain region are listed by ESA or are identified as stocks at varying degrees of risk by Nehlsen *et al.* (1991) or The Wilderness Society (1993). The exception is summer steelhead in the Grande Ronde, which is identified as stable (The Wilderness Society 1993). Anadromous runs to both regions are subjected to the effects of 8 to 10 mainstem Columbia River dams.

Conclusions

From these snapshots over time, it is apparent that the response of fish habitat to differing natural and human-induced disturbances varies greatly. Although precise, quantifiable relationships between long-term trends in fish abundance and land-use practices are difficult to obtain (Bisson *et al.* 1992), the body of literature concludes that land-use practices cause the simplification of fish habitat (Hicks *et al.* 1991, Bisson *et al.* 1992, Meehan 1991)

The conclusions of this paper must be viewed with caution. A broad regional overview of this nature can fail to identify known areas of concern. A few anadromous stocks in the Mid-Columbia region are at risk, especially steelhead (Mullan *et al.* 1992, Nehlsen *et al.* 1991, The Wilderness Society 1993). Alternatively, most anadromous runs to the Mid-Columbia region are stable (Mullan *et al.* 1992, The Wilderness Society 1993). In the Blue Mountain region, few anadromous runs are stable; most are severely depressed and declining (Nehlsen *et al.* 1991, The Wilderness Society 1993). The results of this study suggest that this difference may be due to better habitat conditions in the Mid-Columbia region.

Strategies to protect and restore anadromous and resident fish habitat must be based on a watershed approach that protects the remaining habitat and restores historical habitats (Johnson *et al.* 1991, Reeves and Sedell 1992, USDA 1993). The Forest Service is currently developing such a strategy (PACFISH) to be applied across the range of anadromous salmonids throughout the western United States (USDA Forest Service 1992b). Management plans addressing forest health in eastern Oregon and Washington must explicitly incorporate a watershed strategy that recognizes the critical linkages between the uplands, riparian areas, fish habitat, and fish populations. Land

management activities that contributed to the forest health problem (i.e., selective harvest and fire suppression) have had an equal or greater effect on aquatic ecosystems. If we are to restore and maintain high-quality fish habitat, then protecting and restoring aquatic and terrestrial ecosystems is essential.

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